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Josie Hughes, Andrew Fall, Les Safranyik and Ken Lertzman

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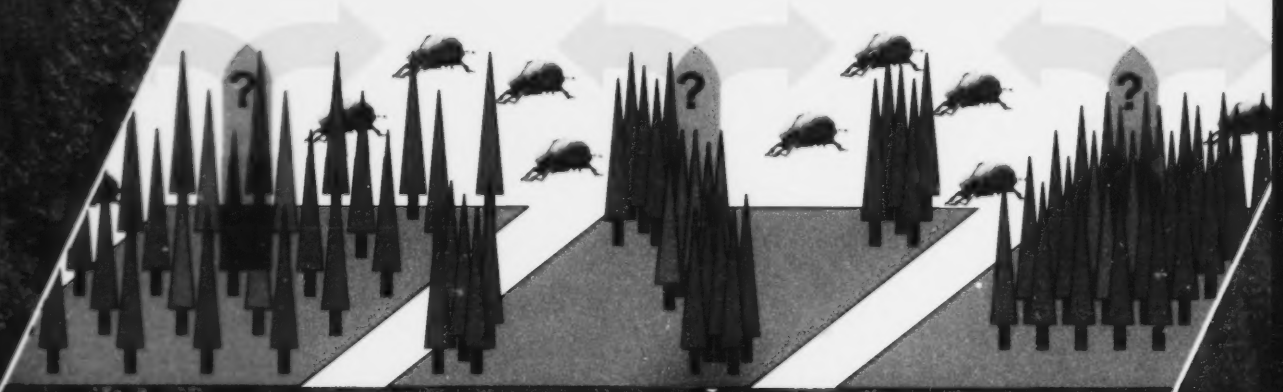

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Modeling the effect of landscape pattern on mountain pine beetles

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Contents

Abstract / Résumé v

1.0 Introduction 1
1.1 Management context and motivation 1
1.2 Terminology 1
1.3 Expectations 1
1.3.1 Effect of pattern in general 1
1.3.2 Consequences of pheromone mediated aggregation 3
1.3.3 Consequences of free flight 4
1.4 Overview and objectives 4
2.0 Methods 6
2.1 The model 6
2.2 Experimental design and analysis 6
2.2.1 Pattern generation and experimental design 6
2.2.2 Analysis Procedure 7
3. Experiments and results 10
3.1. The model 10
3.1.1. Notation 10
3.1.2. Conceptual overview of the flight model 10
3.1.3. Mountain pine beetle mode changes 10
3.1.4. Mountain pine beetle movement 12
3.1.5. Landing and pheromone production 13
3.1.6. Pheromone diffusion and decay 14
3.1.7. Complete model of dispersal, aggregation and attack 15
3.1.8 Extending the model over multiple years 15
3.1.9. Base model parameterization 16
3.1.10 Numerical methods and model implementation 19
3.1.11 Temporal extent and resolution 20
3.1.12 Initial conditions 20
3.2 Clarifying hypotheses 21
3.3 Experiment I – base case 23
3.4 Experiment II – the effect of free flight 25
3.5 Experiment II extension – sensitivity without free flight 27
4. Discussion 29
4.1. Beetle ecology 29
4.2. Movement modeling 30
Acknowledgements 31
References 32
Tables 38
Appendix 44

Tables

1A. Definitions of terms 38
1B. Definitions of terms (continued). 39
2. Probabilities for transitions between five beetle modes 40
3. Model parameters and their associated base values. 41
4. Summary of experimental results 43

Figures

1. The potential effects of changing habitat configuration 2
2. Experimental design scheme. 7
3. Sensitivity of Weibull-type curve to shape parameters 8
4. Summary of model within the flight period 11
5. Distances flown by modeled mountain pine beetles 18
6. Sensitivity of pheromone plume size and shape 19
7. Definition and calculation of center cluster size. 21
8. The effect of habitat compaction, patch size, and communication distance on center cluster size 22
9. Pheromone plumes used in base experiment 23
10. The effect of habitat compaction, patch size, and communication distance on kill rate in the base case. 24
11. The effect of habitat compaction and communication distance on the number of outbreaks in the base case 25
12. The effect of habitat compaction, patch size, communication distance and *free flight* on kill rate in Experiment II.. 26
13. The effect of habitat compaction, patch size and free flight on the number of outbreaks in Experiment II. 26
14. The effect of winter reproductive rate on results from Experiment II. 27
15. The effect of winter reproductive rate on results from Experiment II. 28

A.1. Effect of the parameter α_{μ} on turning angles in free flight 44
A.2. The sensitivity of attractiveness to the gradient sensitivity parameters 45
A.3. Sensitivity of relative attractiveness of pheromones to pheromone gradient *and* the gradient sensitivity parameters 46
A.4. Sensitivity of the relationship between per beetle landing rate and the number of nesting beetles to host resistance 47
A.5. Sensitivity of landing rate to six model parameters 48
A.6. Sensitivity of per beetle and per area pheromone production rates to host resistance 49
A.7. Sensitivity of pheromone production to three model parameters 50
A.8. Sensitivity of reproductive rate and kill rate to host resistance 51
A.9. Sensitivity of reproductive rate to three model parameters 52
A.10. Sensitivity of reproductive rate to three model parameters 53

Abstract

Despite ecological and management importance, little is known about the effect of forest landscape structure on the spread of mountain pine beetles (*Dendroctonus ponderosae* Hopkins). The general prediction from published literature is that forest fragmentation at some scale might slow the spread of infestations. However, mountain pine beetle dispersal ecology is complicated by requirement for attack *en masse* and a pheromone-based communication system that facilitates this aggregation process. One interesting possibility is that infestations might spread more slowly over habitat gaps across which beetles cannot communicate. To investigate this possibility, we develop an individual-based model of mountain pine beetle dispersal, aggregation and attack, and perform simulation experiments to explore the effects of habitat patch size, habitat compaction, communication distance, and flight behaviour on the spread rate and final extent of infestations. The model is based on a spatially explicit mountain pine beetle model developed by Powell *et al.* (1996, *Mathematical elements of attack risk analysis for mountain pine beetles. Journal of Theoretical Biology* 204(4): 601-620), but differs from that model on several points.

Increasing the distance between patches does slow infestation spread, though not as much as expected. When we remove the tendency of beetles to fly for some period before becoming receptive to pheromones (free flight), patch size becomes important and spread rate only varies with habitat compaction when patch size is small. At face value, the prediction is that beetles will be somewhat sensitive to forest fragmentation at small scales, but insensitive to variation in patch size because of their free flight behaviour. This result is subject to uncertainty about model form and parameterization. More robust aspects of this work include a review of the potential effects of relatively small-scale spatial structure on aggregating organisms, a comparison of diffusion and individual-based modeling approaches, and consideration of some assumptions underlying this and preceding mountain pine beetle models.

Résumé

Malgré son importance sur les plans de l'écologie et de la gestion, on connaît très peu l'effet de la structure du paysage forestier sur la dispersion du dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopkins). La prévision générale se dégageant de différentes publications est que la fragmentation de la forêt à une certaine échelle pourrait ralentir l'infestation. Cependant, l'écologie de la dispersion du dendroctone du pin ponderosa est compliquée par l'exigence d'une attaque massive et d'un système de communication fondé sur les phéromones qui facilite le processus d'agrégation. Une possibilité intéressante est que les infestations pourraient se répandre plus lentement en cas d'écarts entre les habitats qui empêchent les scolytes de communiquer. Afin d'étudier cette possibilité, nous mettons au point un modèle individualisé de dispersion, d'agrégation et d'attaque du dendroctone du pin ponderosa, et nous effectuons des expériences de simulation dans le but d'explorer les effets de la taille de la parcelle d'habitat, de la compacité de l'habitat, de la distance de communication et du comportement de vol sur la rapidité de propagation et l'étendue finale des infestations. Ce modèle repose sur un modèle spatialement explicite du dendroctone du pin ponderosa mis au point par Powell et al. (1996, *Mathematical elements of attack risk analysis for mountain pine beetles. Journal of Theoretical Biology* 204(4): 601-620), mais il en diffère à plusieurs égards.

L'augmentation de la distance entre les parcelles ralentit la vitesse d'infestation, mais pas autant que l'on pensait. Lorsque nous éliminons la tendance des dendroctones à voler pendant un certain temps avant d'être réceptifs aux phéromones (vol libre), la taille de la parcelle devient un facteur important et la vitesse de propagation varie uniquement en fonction de la compacité de l'habitat si la parcelle est de petite

taille. À l'origine, la prévision est que les insectes seront sensibles en quelle que sorte à la fragmentation de la forêt à petite échelle, mais qu'ils seront insensibles à la variation de la taille de la parcelle en raison de leur comportement en vol libre. Ce résultat dépend de l'incertitude liée à la forme et au paramétrage du modèle. Les aspects plus solides de ces travaux incluent une révision des effets possibles d'une structure spatiale relativement petite sur les organismes qui se regroupent, une comparaison des approches de modélisation individualisée et de la diffusion, ainsi qu'une étude de certaines hypothèses sur lesquelles reposent ce modèle et les modèles antérieurs d'étude du dendroctone du pin ponderosa.

1.0 Introduction

1.1 Management context and motivation

Mountain pine beetles (*Dendroctonus ponderosae* Hopkins) are a major agent of lodgepole pine (*Pinus contorta* Dougl. ex Loud. Var. latifolia Engelm.) mortality, and have therefore been a subject of intense research and management effort for over 100 years (Amman and Logan 1998). Population models (Berryman 1978; Clark et al. 1979; Thompson et al. 1981; Raffa and Berryman 1986; Mawby et al. 1989; Safranyik et al. 1999) and more general understanding of system dynamics (Ludwig et al. 1997) predict that outbreaks should be easier to prevent than to control. A long history of failed or dubiously successful control efforts (Wood et al. 1985; Amman and Logan 1998) is consistent with the theory, prompting calls for more proactive management (Amman and Safranyik 1985; Amman and Logan 1998; Samman and Logan 2000).

Lodgepole pine trees become susceptible at 60 to 80 years of age. Thus, one way to prevent mountain pine beetle outbreaks is to remove older pine from the forest (Amman et al. 1984; Amman and Safranyik 1985; Maclauchlan and Brooks 1994). Older forests tend to have high biodiversity, wildlife, recreation and other non-timber values, so a strategy to reduce the susceptibility of a landscape to beetle outbreaks while retaining old forest may best meet societal goals.

Some promise for slowing beetles while retaining pine lies in the consideration of landscape pattern and spatial heterogeneity. For instance, increasing the heterogeneity of landscapes may decrease the rate of spread and extent of disease outbreaks and disturbances (Turner et al. 1989; Rodriguez and Torres-Sorando 2001), decrease the survival and reproductive rates of some organisms (Simberloff 1988; Cantrell and Cosner 1991; Saunders et al. 1991; Andren 1994; Bender et al. 1998; Heibeler 2000), and globally stabilize locally unstable population dynamics (Hastings 1977; May 1978; Reeve 1988; Taylor 1990). In forests, the juxtaposition of stands of different age classes can reduce overall landscape flammability (Franklin and Forman 1987; Turner and Romme 1994; Turner et al. 1999), and isolated forest patches suffer less damage from the eastern spruce budworm (*Choristoneura fumiferana*) (Cappuccino et al. 1998). The effect of landscape pattern depends on complex interactions between a landscape and the habitat preferences and dispersal ecology of individual species (Saunders et al. 1991; Andren 1994; Coulson et al. 1999). For specific predictions it is necessary to consider some details of mountain pine beetle ecology.

1.2 Terminology

Throughout this paper we use concepts and terms from the field of landscape ecology (e.g. *landscape*, *patch*, *spatial heterogeneity*), and from population ecology or entomology (e.g. *infestation*, *outbreak*, *aggregation*). Terms common in these fields may not be familiar to a wider audience, and even within a field some confusion may arise. We also have coined a few terms specifically for use in this paper (e.g. *free flight*, *communication distance*, *habitat compaction*). Concepts and terms specific to this paper are explained as they arise throughout this text, and are also included in Table 1b for reference. Concepts and terms common to either landscape ecology or population ecology may not be defined in the text, but are explained with references in Table 1a,b for the convenience of readers.

1.3 Expectations

1.3.1 Effect of pattern in general

First, we are concerned with a narrow range of effects arising from variation in the spatial arrangement of habitat. Changing forest pattern can significantly affect radiation fluxes, wind patterns, water fluxes,

predator abundance, and other aspects of the ecosystem (Saunders 1991) that might in turn affect mountain pine beetles. We do not consider such indirect effects.

Models of simple epidemics with removal (SIR – Susceptible/Infective/Removed) are standard in epidemiology (see Capasso 1993 for overview). In these models, disease is transmitted from infective to susceptible individuals, which then become infective. After some period, infective individuals either die, or recover and become resistant to the disease. Since mountain pine beetles kill their hosts as they spread, results from SIR models may be relevant.

Bolker (1999) examined the effect of host spatial heterogeneity, or patchiness, on the spread of an SIR type disease through plant populations. He used analytic and stochastic simulation models to demonstrate that clustering hosts in space can increase both the spread rate and the final size of epidemics, while even spacing of host plants may decrease rate of disease spread (Figure 1a). This result is consistent with previous theoretical work in epidemiology, and the effect has also been observed in several experimental studies (Bolker 1999).

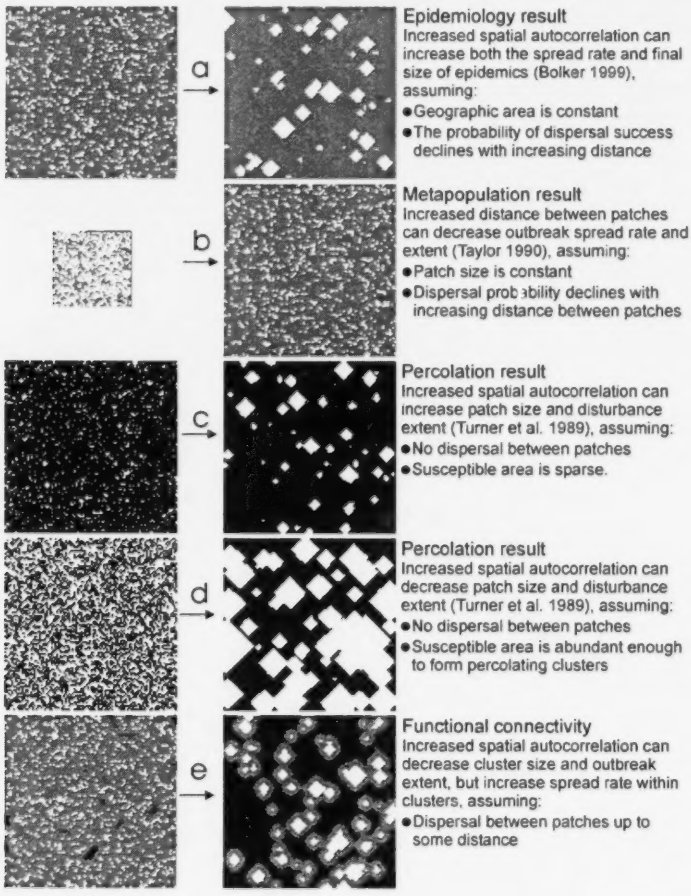
a
b
c
d
e
Epidemiology result
Increased spatial autocorrelation can increase both the spread rate and final size of epidemics (Bolker 1999), assuming:
•Geographic area is constant
•The probability of dispersal success declines with increasing distance
Metapopulation result
Increased distance between patches can decrease outbreak spread rate and extent (Taylor 1990), assuming:
•Patch size is constant
•Dispersal probability declines with increasing distance between patches
Percolation result
Increased spatial autocorrelation can increase patch size and disturbance extent (Turner et al. 1989), assuming:
•No dispersal between patches
•Susceptible area is sparse.
Percolation result
Increased spatial autocorrelation can decrease patch size and disturbance extent (Turner et al. 1989), assuming:
•No dispersal between patches
•Susceptible area is abundant enough to form percolating clusters
Functional connectivity
Increased spatial autocorrelation can decrease cluster size and outbreak extent, but increase spread rate within clusters, assuming:
•Dispersal between patches up to some distance

Figure 1: The potential effects of changing habitat configuration depend on organism dispersal ability, habitat abundance, and whether total geographic extent is allowed to vary. Suitable habitat (or susceptible area, for consideration of non-biological disturbances) is white, unsuitable habitat within the dispersal range of an organism is grey, and unsuitable non-traversable area is black.

A central result in metapopulation theory is that increasing the distance between sub-populations can allow regional stability of locally unstable predator-prey interactions by limiting the extent of local population oscillations or outbreaks (Taylor 1990) (Figure 1b). The different predictions from metapopulation and epidemiological work are partly due to different reference conditions. The epidemiologists assume that average initial transmission rate, or the initial ratio of hosts to non-hosts, is constant, so their finding is that epidemics spread faster when hosts are aggregated than when hosts are dispersed randomly over the same geographical area (Figure 1a). In contrast, the metapopulation studies are concerned with increasing the isolation of (or distance between) host patches, so they hold patch size constant and increase the distance between hosts or, effectively, the geographic area across which hosts are dispersed. Increasing the distance between patches will tend to slow the spread of organisms, given constant patch size (Figure 1b). If geographic area is constant, the average distance between the edges of round patches can only be increased by making patches larger, which increases spread rate.

The epidemiological and metapopulation models discussed so far assume that dispersal may occur between patches. In the other extreme, classic percolation models assume that agents cannot spread across gaps between habitat patches, so the total extent of an outbreak or disturbance is absolutely constrained by the size of habitat patches (Turner et al. 1989). In these models, we observe a threshold effect; at intermediate habitat abundance, small increases in habitat can dramatically increase disturbance extent by linking large patches. Percolation models also emphasize that the effect of increased patchiness should depend on the relative abundance of habitat - if habitat is abundant, increased clumping may decrease average patch size and outbreak extent isolating patches from one another (Figure 1d). In contrast, if habitat is sparse, increased clumping may increase patch size and outbreak extent (Figure 1c). Empirical studies of birds and mammals support the general conclusion that pattern effects depend on the relative abundance of habitat (Andren 1994).

In most situations, the dispersal reality is probably somewhere between two extremes. No organisms can traverse infinite distances, but most can travel some distance through inhospitable area. Thus, the "functional connectivity" of habitat is less than infinite, and more than the physical connectivity of habitat patches (Tischendorf and Fahrig 2000). Keitt et al. (1997) have highlighted that clusters of habitat patches separated by less than dispersal distance may be linked into percolation clusters by dispersal. Decreasing average cluster size should decrease the average size of outbreaks (Figure 1e). Within clusters, increasing patch size might increase spread rate as predicted by epidemiological models.

1.3.2 Consequences of pheromone mediated aggregation

Pine resists beetle attack by secreting resin that physically impedes progress, interferes with pheromone signals, seals the living cells from infection by fungus, and drowns eggs and larvae. [For overviews of mountain pine beetle biology see Amman (1978), Amman et al. (1984), Safranyik (1989), and Samman and Logan (2000)]. To overcome host defenses, beetles must attack in large groups. To facilitate mass attack, beetles disperse synchronously over a period of two to three weeks, and use a system of at least five different pheromones to attract others to areas where attack is insufficient, and later repel from areas that are full (see Borden et al. 1987 for review). In entomological literature the process is termed pheromone-mediated aggregation (and attractive pheromones are aggregative). In a more general context, Turchin (1998) distinguishes between aggregative behaviour, where organisms orient toward suitable hosts or some other attractor, and congregative behaviour, where organisms orient toward one another. We note that from this perspective, mountain pine beetle dispersal is functionally more like congregation than aggregation. Throughout this document we use the term aggregation to remain consistent with entomological literature.

Discussions of functional connectivity often focus on dispersal ability as the limiting factor (Keitt et al. 1997; Tischendorf and Fahrig 2000). However, if aggregation is required for success then landscapes across which organisms cannot effectively aggregate will be fragmented, whether or not individuals can move from patch to patch. For mountain pine beetles, functional connectivity may depend on the scale

of pheromone communication, and fragmentation at the scale of pheromone communication may alter the rate and extent of infestation spread. Others have also suggested that attraction between conspecifics might affect population dynamics (Smith and Peacock 1990; Turchin 1989).

1.3.3 Consequences of free flight

The spatial aspect of mountain pine beetle population ecology has intrigued other authors, and other spatially explicit beetle models have been built. Most have taken a continuum reaction-diffusion approach, where movement is approximated by a simple diffusion or advection-diffusion process, written as a partial differential equation (Polymenopoulos and Long 1990; Turchin and Thoeny 1993; Logan et al. 1998). The model most applicable here is by Powell, Logan, Bentz and others (referred to as the MPBpde) (Powell et al. 1996; White and Powell 1997; Logan et al. 1998; Powell et al. 1998; White and Powell 1998; Powell et al. 1999; Biesinger et al. 2000; Powell et al. 2000 – for simplicity, this group of citations will be referred to collectively as Powell et al. through the remainder of this document). The MPBpde is the starting point for our model.

The diffusion approach has several advantages, including generality, flexibility, and analytical tractability (Okubo 1980; Turchin 1991, 1998). The mathematics are well understood, and behavioural assumptions are clear and explicit. However, not all movement behaviours can be handled with a diffusion approach. For example, many bark beetle species require some period of exercise, or "free flight", before they become responsive to pheromones (Borden et al. 1986). Field studies of *Ips typographus* suggest that free flight periods may significantly alter dispersal patterns (Helland 1984; Helland 1989), and indirect evidence for the effect on mountain pine beetle dispersal is given by the fact that some beetles fly past nearby attractive sources (Safranyik et al. 1989), and that infestations tend to spread before all the hosts within an infested area are depleted (Mitchell and Preisler 1991; Borden 1993). In diffusion approximations, individuals are considered in aggregate. Unless all beetles emerge at the same time, one cannot model changes in behaviour that depend on time since emergence with a diffusion approach. Since mountain pine beetles emerge throughout the flight period, a diffusion approximation cannot capture the free flight behaviour. We wish to know whether adding free flight fundamentally alters the results of interest.

Continuum reaction-diffusion models are just one among a range of options for modeling movement (Turchin 1998). At the other extreme, in individual-based models organisms move independently of one another. The individual-based approach allows more flexible movement rules, and the implementation of these rules is largely intuitive. However, individual-based models are often difficult to analyze and communicate (Grimm et al. 1999). Greater flexibility is not always a virtue, making models difficult to compare, and less conducive to general insight (Turchin 1998; Grimm 1999; Grimm et al. 1999). Neither approach is perfect, and the best choice depends on the question. Here, we are interested in whether free flight behaviour alters the effect of landscape pattern on mountain pine beetles. Since free flight behaviour cannot be modeled with a diffusion approximation we take an individual-based approach.

1.4 Overview and objectives

Our overall objective is to understand the effect of habitat distribution on the dispersal and success of mountain pine beetles. The key hypothesis is that relatively short gaps between habitat patches might disrupt mountain pine beetle and reduce success because pheromone-based communication is important for success, and beetles communicate effectively across shorter distances than they fly. We refer to the maximum distance across which pheromones effectively spread and beetles effectively communicate as "communication distance". To explore this hypothesis, we first develop a simulation model of mountain pine beetle dispersal, aggregation, and success, building on the work of Powell et al. We simulate a set of landscape patterns that vary in the size of habitat patches (w), and the area across which habitat is dis-

persed (habitat compaction, p). Next, we ask how landscape pattern affects beetles in a set of simulation experiments. We look at the effect of pattern on beetles given the best available estimates of all model parameters. We then consider the sensitivity of model behaviour to two key parameters – the tendency of beetles to fly for some distance before becoming receptive to pheromones, and the over-winter reproductive rate of beetles.

2.0 Methods

2.1 The model

The simulation model is based on review of knowledge about mountain pine beetle dispersal ecology, and existing beetle models. The synthesis and perspective gained through model development is a key result of this study, so model details are presented in the results section of this paper. However, it is useful to define spatial extent and resolution immediately. These basic decisions about model structure set the context for experimental design and model form decisions to follow.

First, average beetle dispersal distance under a canopy is less than 1 km, and most beetles seem to travel less than 3 km (Safranyik et al. 1989; Turchin and Thoeny 1993). At the other end of the scale, experience with baited pheromone traps suggests that pheromone plumes effectively extend over distances of 50-100 m (Borden, J. Chief Scientific Officer, Pherotech International Inc., 7572 Progress Way, Delta, BC, V4G 1E9). By these indications, our simulated experimental landscapes should be over 3 km in extent (to avoid excessive edge effects in beetle dispersal), with a grid-cell resolution of at least 50 × 50 m (to resolve pheromone dynamics). We chose a spatial extent of 5 × 5 km, or 2500 ha, and grid cell resolution of 50 × 50 m, or 0.25 ha cell^{-1}. Running all simulations on a square landscape of 5 × 5 km, resolved at 0.25 ha cell^{-1}, gives a total of 10,000 cells per landscape.

2.2 Experimental design and analysis

2.2.1 Pattern generation and experimental design

Binary landscapes were created using a spreading algorithm modified from a simple fire model (Fall 1998). Habitat patches are placed at random, subject to the constraint that new patches cannot start within old ones. Patch sizes are chosen from a Weibull distribution. Each patch spreads from a starting cell up to the chosen size, and the complexity of patch shape depends on the number of neighbours to which each cell spreads in each step. New patches do not spread over old ones, but spreading may continue until patches adjoin. Note that because patches may adjoin (fuse) the actual patch size distribution may differ from the target (Weibull) patch size distribution. Patches are initiated and spread sequentially until the proportion of habitat within the landscape reaches a predetermined level. The (target) distribution of patch size is controlled directly by the Weibull scale (θ) and shape (γ) parameters. The probability of spreading to a given number of neighbours is normally distributed. We further constrained patterns by insisting that the first patch initiate in the centre of each landscape.

Landscape fragmentation, or, for the purposes of this discussion, the average minimum distance between patches, can be affected by changing patch size, changing the amount of habitat within a given area, or changing the area occupied by a given amount of habitat (habitat compaction). We are interested here in the effects of spatial arrangement, rather than quantity, so we kept total habitat supply constant at 5% of the landscape (i.e. 250 ha out of 5000 ha). We used a multi-factorial experimental design, with four levels of average patch size (w) from small (0.39 ha) to large (14.2 ha), four levels of habitat compaction (p) from 10 to 40 % of the landscape at intervals of 10 %, and five replicates of each resulting pattern type (Figure 2). Parameter values were chosen so the range of fragmentation scales (measured as average minimum distance between patches) spans the range of pheromone communication scales (<50 m to >200 m).

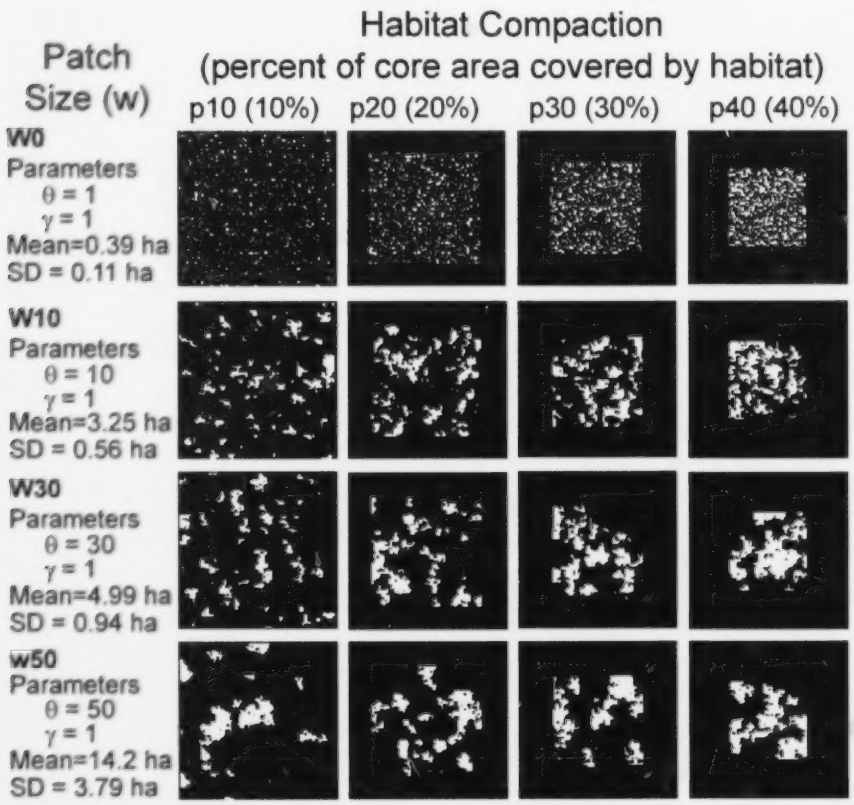

Figure 2: Experimental design scheme showing variation in patch size and patch compaction. Five percent (250 ha) of each landscape is habitat. Weibull scale parameter (θ) is varied and the shape (γ) of the distribution remains constant. The mean and standard deviation (SD) are given for the case where habitat compaction is low (p10). Realized patch size will increase with habitat compaction as close patches merge. There are five replicates of each pattern, one of which is shown here. Communication distance and other experimental factors are repeated within pattern in a split plot experimental design.

2.2.2 *Analysis Procedure*

The output from each model run is a 25-year time series of area killed per year. Area killed ranges from 0 to 250 ha or 100%. Output curves are characteristically sigmoidal; if conditions allow mountain pine beetles to overcome host defenses then outbreak extent increases exponentially until beetle populations are limited by habitat supply. We fit a three-parameter Weibull-type curve (from Ratkowsky 1990) to each output series (kill vs. time), and then treat the estimated coefficients of each regression as multiple response variables that can be analyzed using standard regression techniques (Cook and Ware 1983). The Weibull-type curve is:

$$y = a_w(1 - e^{-e^{-g_w X^{d_w}}})$$

Increasing either g_w or d_w increases the slope of the curve (Figure 3). We analyze the maximum area killed after 25 years ($kill_t$) rather than the estimated asymptote (a_w) because curves that are low but slowly

increasing at the end of the simulation do not provide enough information for a meaningful asymptote estimate. Scale (a_w) is fixed at 100%. Note that rigorous model selection is not a great concern, as the models are used to describe curves, rather than to predict. If the fit is adequate then comparison of the curves should be consistent regardless of the model used (Potvin et al. 1990).

The parameters g_w and d_w are distributed so that a continuous statistical modeling approach is appropriate. The maximum area killed, in contrast, is bimodally distributed. In 15 % of runs, beetles kill less than 20% of habitat over 25 years. Otherwise, beetles kill more than 90% of habitat. To avoid violating regression assumptions we converted this area killed response to a binomial variable by classifying all cases as either "outbreak" (>90% of available habitat killed) or "non-outbreak" (< 90% killed). Because beetles always kill <20% or >90% of available habitat it makes no difference which threshold between 20 and 90% we choose to distinguish outbreak from non-outbreak cases.

We varied communication distance (the maximum distance across which pheromones effectively spread and beetles effectively communicate) and other model parameters within each instance of pattern, so the experiments have a repeated measure or split-block design. The two kill rate responses were analyzed using mixed models to avoid violating the restrictive circularity assumption of randomized block or split-plot ANOVA (von Ende 2001). Patch size and shape are between-subject factors, and all other experimental factors are repeated within pattern. Unstructured covariance matrices were assumed, and all response values were log transformed to equalize variance between groups.

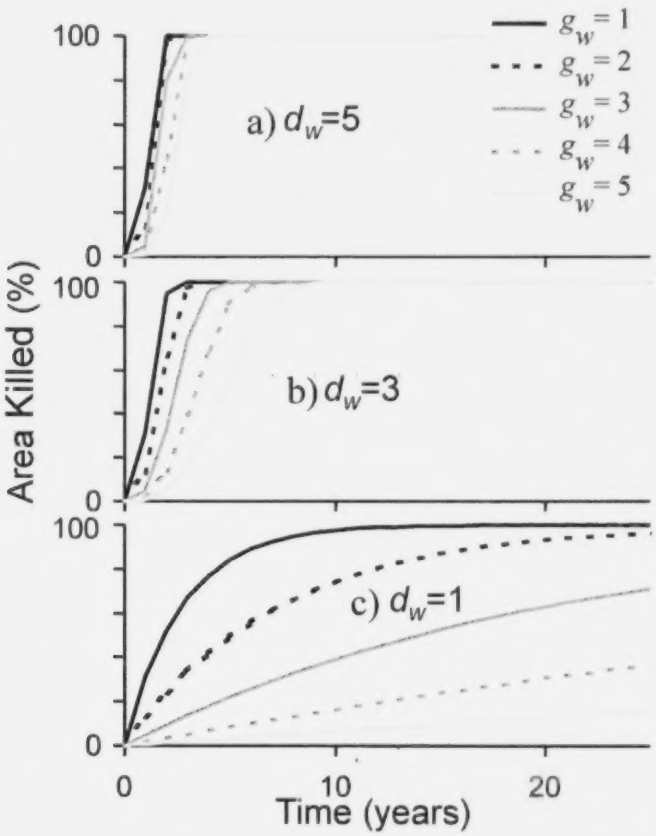

Figure 3: Sensitivity of Weibull-type curve to shape (g_w and d_w) parameters.

Analyzing the binary outbreak data was more difficult. In general, levels of communication distance are not independent; if beetles can outbreak when communication distance is short they are nearly certain to outbreak at larger communication distances. However, lack of variation in response at some levels of communication distance prevents the estimation of more appropriate covariance matrices, leaving us in the ironic position of being unable to analyze the data properly because the experimental effects are too strong. Being unable to fit an appropriate repeated measures model, we pooled the three repeated measures into one response variable by counting the number of outbreaks that occurred on that pattern across all levels of communication distance. We tested for effects of patch size and habitat compaction on this overall chance of an outbreak by fitting a mixed model, assuming the random variable is Poisson distributed, and specifying a log link function (Agresti 1996). Sampling zeros and lack of variation at some levels were corrected by adding a small amount (0.001) to each outbreak count.

Post-hoc comparisons were challenging due to the large number of possible pair-wise comparisons (4560 in the base experiment with four levels of patch size, four levels of habitat compaction, three levels of communication distance, and two response variables). We compared each group mean to the maximum and minimum group means in the experiment to see which kill rates were significantly greater than "low" or significantly less than "high". Although we only examined a subset, all pair-wise comparisons are adjusted for the full set of comparisons using the Tukey-Kramer method.

Data manipulations and non-linear regressions were done with S+ using the NLREGB function (Insightful Corp. 2001, S-Plus V.6.1.Seattle, WA). Continuous mixed models were fit using the MIXED procedure in SAS, and multinomial mixed models were fit using the GENMOD procedure (SAS Institute Inc. 2000, SAS V.8.1, Cary, NC).

3.0 Experiments and results

3.1. The model

The annual cycle of the mountain pine beetle can be broadly divided into two parts: the flight period, consisting of several weeks when beetles emerge, disperse, and attack new hosts; and the rest of the year, when beetles feed, mate, and reproduce under the bark of host trees. We describe the model of mountain pine beetle dispersal within a single flight period, then describe how the model is extended over multiple years.

3.1.1. Notation

State variables (e.g., the number of flying beetles, F) in this model vary across space and time, so the value of variable F at location (i,j) and time t is $F_{i,j,t}$. For convenience, in most cases we drop the subscript notation on state variables, which are denoted by capital letters. Model parameters are aspatial constants unless otherwise noted. Probabilities are denoted using P( ).

3.1.2. Conceptual overview of the flight model

Each individual beetle can be in one of five possible modes: *waiting* to emerge, flying and unreceptive to pheromones (*uflying*), flying and receptive to pheromones (*rflying*), *nesting* after landing, or *dead*. Nesting beetles are beetles that have committed to staying at a location; once a beetle is nesting it does not return to flying. Each beetle also has a location, and flying beetles may remain within the current cell or move to one of eight neighbouring locations on the square lattice representing the area under consideration. Nesting beetles produce pheromones, to which receptive flying beetles respond. See Figure 4 for a schematic model overview of the flight model.

Following Powell et al., the change in pheromone concentration (A) over space and time is the sum of production, diffusion, and decay (or loss through the canopy). Like Powell et al., we also consider the resistance of forest R, which varies between 0 and 1, but in our model R is static over the flight period. We have added a second forest variable K to explicitly represent carrying capacity for beetles at each location. By making capacity for beetles explicit, rather than an emergent property of resin depletion, we can ensure areas with little resistance (and few trees) become repulsive to beetles at some point, while areas with high resistance (and many trees) do not become repulsive before resistance is depleted.

3.1.3. Mountain pine beetle mode changes

The state of beetle k at time t is given by its mode $\Omega_{k,t}$ (*waiting*, *uflying*, *rflying*, *nesting*, or *dead*) and location Lock,t (row and column). One mode transition per beetle may occur each time-step. The beetle time-step, Δt, is the temporal resolution of the beetle simulation. Δt must be set small enough that beetles land or die at a rate of less than 100% per Δt, and travel at a rate of less than 1 grid cell per Δt. We consider an appropriate value for Δt in section 3.1.11, once death, landing and movement rate parameters have been defined. The conditional probability of transition to mode $\Omega_{k,t}$ given that the beetle was in mode $\Omega_{k,t}$-Δt at time t-Δt is written as $P(\Omega_{k,t} \mid \Omega_{k,t-\Delta t})$. All but ten mode transition probabilities are zero (Table 2). The probability of a beetle remaining in the same mode is one minus the sum of the probabilities for mode change.

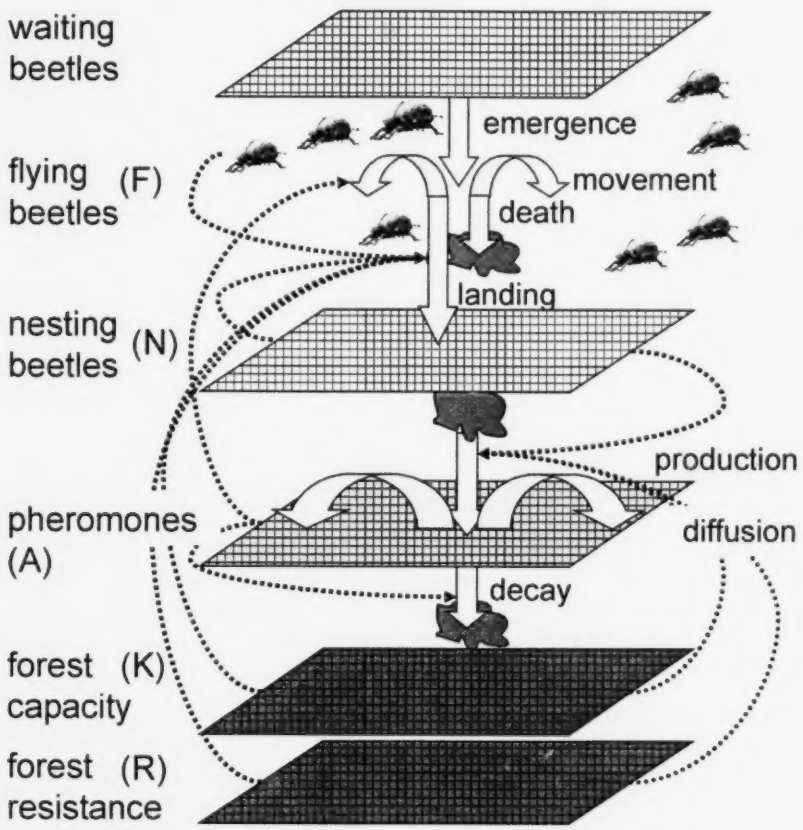

Figure 4: Summary of model within the flight period. Continuous state variables are represented by grids, while individually modeled flying beetles are drawn separately. Descriptions of each state variable are given on the left hand side, with variable names following in brackets. Material flows of pheromones and beetles are indicated by white block arrows. Flows can either be between states (beetles only, vertical arrows), between locations within the same state (curved arrows), or between the modeling system and the external world (vertical arrows beginning or ending in clouds). Flow processes are labeled on the right hand side. Black dotted arrows indicate the effects of state variables on flow rates.

Following Powell et al., we assume that beetles emerge at a uniform rate over the flight period. In truth, emergence patterns depend on temperature patterns over the flight-period and the preceding year, with typically fewer beetles emerging near the beginning of the flight period (Bentz et al. 1991; Safranyik and Linton 1993). The probability of a waiting beetle emerging at a particular time is the inverse of the total flight period: $P(\Omega_{k,t} = uflying \mid \Omega_{k,t-\Delta t} = waiting) = \Delta t / p_f$. We assume that waiting beetles represent the number of emergers, so no mortality is applied to this mode. Also following Powell et al., we assume a constant flying death rate: $P(\Omega_{k,t} = dead \mid \Omega_{k,t-\Delta t} = uflying \text{ or } rflying) = \Delta t \omega_1$.

To include the free flight mechanism, we follow Helland et al. (1984) and assume that mountain pine beetles are unreceptive to pheromones upon emergence, and unreceptive beetles (*uflying*) become receptive (*rflying*) at a constant rate: $P(\Omega_{k,t} = rflying \mid \Omega_{k,t-\Delta t} = uflying) = (1 - \Delta t \omega_1) \Delta t \, r_f$.

Unreceptive beetles neither land nor respond to chemical cues. Receptive beetles may land with a certain probability, which we discuss in detail in the next section. For now, it suffices that $P(\Omega_{k,t} = nesting \mid \Omega_{k,t-\Delta t} = rflying) = \Delta t \; landing\ rate_{i,j,t}$, which depends on the dynamic characteristics of the beetle location (i,j). In reality, beetles land at night when the temperature falls, and return to

flying the next day. We skip over these night-resting periods, and allow beetles to fly continuously through the flight period. Once a beetle has landed it does not return to flying, and nesting death is included in the assessment of over-winter survival and success, so $P(\Omega_{k,t} = nesting \mid \Omega_{k,t-\Delta t} = nesting) = 1$. Clearly, dead beetles remain so.

3.1.4. Mountain pine beetle movement

If flying beetles neither die nor land in a time step, they may make one move. The probability of a beetle moving to a location at time t given its state $\Omega_{k,t}$ (where $\Omega_{k,t}$ = *uflying* or *rflying*) and its location at time t-Δt is denoted $P(Loc_{k,t} = (i+m, j+n) \mid \Omega_{k,t} \;\&\; Loc_{k,t-\Delta t} = (i,j))$ where i and j are the row and column location of the beetle at time t- Δt, and n and m are integers belonging to the set {−1,0,1}.

Scolytids tend to fly down or across wind until they encounter a pheromone plume, and follow plumes upwind to their source (Choudhury and Kennedy 1980; Byers 1988; Safranyik et al. 1989). Also, in the absence of pheromones beetles preferentially select some hosts based on bole size or host volatiles (Gara et al. 1984). We do not include these complications in the dispersal model. However, Zollner and Lima (1999) have shown that straight or nearly straight search strategies are more efficient than purely random ones. To ensure that search efficiency of beetles is not excessively underestimated, we assume that unreceptive beetles follow a correlated random walk search pattern:

$$P\{Loc_{k,t} = (i+m, j+n) \mid \Omega_{k,t} = uflying \;\&\; Loc_{k,t-\Delta t} = (i,j)) = \frac{e^{\frac{-(1-\cos(\alpha_{k,i+m,j+n,t}))}{(1-\cos(\alpha_m))}}}{\sum_{g=-1}^{1}\sum_{h=-1}^{1} e^{\frac{-(1-\cos(\alpha_{k,i+g,j+h,t}))}{(1-\cos(\alpha_m))}}} \quad (1)$$

$\alpha_{k,i+m,j+n,t}$ is the angle between the last move and the potential move (proposed turning angle). The quantity $(1\text{-}cos(\alpha_{k,i+m,j+n,t}))$ is exponentially distributed with the parameter α_m, which is approximately equal to the average turning angle when α_m is small (~<60°). Average turning angle does not continue to increase indefinitely with α_m because the finite range of possible turning angles truncates the exponential distribution. See Figure A.1 for the form of Equation 1.

If there is no difference in pheromone concentration between the current location of a beetle and any of the eight neighbouring cells (ΔA = 0), receptive beetles move like unreceptive beetles (Equation 1). Otherwise, receptive beetles respond to pheromone gradients, or local differences in pheromone concentrations over space. The probability of movement to each location is the relative attractiveness of that location (Figures A.2 and A.3):

$$P(Loc_{k,t} = (i+m, j+m) \mid \Omega_{k,t} = rflying \;\&\; Loc_{k,t-\Delta t} = (i,j) \;\&\; \Delta A \neq 0) = \frac{Attractiveness_{i+m,j+n,t}}{\sum_{g=-1}^{1}\sum_{h=-1}^{1} Attractiveness_{i+g,j+h,t}}$$

$$\text{where } \Delta A = \sum_{g=-1}^{1}\sum_{h=-1}^{1} \mid A_{i,j,t} - A_{i+g,j+h,t} \mid \quad (2)$$

$$Attractiveness_{i+m,j+n,t} = (A_{i+m,j+n,t} + \frac{a_r}{a_s - 1})^{a_t} \quad (3)$$

$A_{i,j,t}$ is the concentration of pheromones at location (i,j) and time t, a_r is the minimum concentration of pheromones detectable by beetles, and as determines the relative preference of beetles for low-pheromone over no-pheromone areas. The attractiveness parameter, a_t, controls the sensitivity of mountain pine beetles to pheromone gradients. The attractiveness function is designed to make beetles more sensitive to differences in pheromone concentration when pheromone concentrations are low.

Note that beetles interpret pheromones differently in this model than in the MPBpde (Powell et al.). Here, pheromones are always attractive (Equation 3), while in that other model very high pheromone concentrations are unattractive. See the following section for reasoning behind this change.

3.1.5. Landing and pheromone production

Mountain pine beetles facilitate mass attack using a system of at least five semiochemicals that differ in the messages they carry, and the rates at which they are produced and decay. Modeling the mechanics of this system is not practical, so the goal here is an abstraction of the system that adequately reproduces the large-scale behaviour of beetle populations. Before developing the abstraction, a brief review of mountain pine beetle pheromone ecology is in order. Early in attack, females produce the attractive pheromone trans-verbenol (Borden et al. 1987). Myrcene and other volatile monoterpenes are released from resin ducts severed by the attacking beetles. Males attracted by this initial combination of volatiles release multi-functional pheromones (exo-brevicomin and frontalin) that are attractive at low concentrations and repulsive at high concentrations. This multi-functionality may help beetles to avoid overcrowding while still promoting enough aggregation to overcome host resistance.

Later in the attack, females stop producing trans-verbenol while males stop producing exo-brevicomin but continue releasing frontalin. Verbenone, an antiaggregant, is produced by autoxidation of trans-verbenol and by microorganisms in association with female beetles. In this last phase, high levels of verbenone and frontalin deter beetles from approaching or landing at the attacked site. The clumped attack patterns and switching behaviour characteristic of mountain pine beetle could be explained by the differential decay rates of verbenone and frontalin. Since verbenone photoisomerizes rapidly on exposure to sunlight (Kostyk et al. 1994), frontalin is likely to diffuse further from the source tree. Beetles would continue to be attracted to those adjacent areas where verbenone was absent and frontalin was present in low (attractive) concentrations.

The net effect is that areas become attractive early in attack, and unattractive later. Powell et al. have chosen to model a single pheromone that is attractive at low concentrations and repulsive at high concentrations. In that model the transition from attraction to repulsion is independent of the resistance and the capacity for beetles at a location. Thus, areas with low capacity (or few trees) may never accumulate enough beetle attacks to become repulsive, while areas with high capacity may become repulsive before enough beetles aggregate to overcome host defenses.

Another consequence of Powell et al.'s formulation is that unattractive areas can create barriers to beetle spread, trapping beetles in poor areas. Real beetles are apparently not so constrained; beetles attack trees baited with verbenone (a repellent) and exo-brevicomin (at attractive concentrations) significantly less than trees baited with only exo-brevicomin, but do not attack verbenone-baited trees less than unbaited trees (Shore et al. 1992). Thus, verbenone effectively masks or neutralizes attractive signals, but does not actively deter beetles.

To avoid erecting pheromone barriers and deterring flying beetles from areas that are not yet full, we assume the antiaggregative effects of verbenone and the multi-functional pheromones remain local within each cell. Thus, areas may cease to be attractive, but never become actively unattractive to dispersal. Once a beetle arrives, antiaggregants will deter it from landing if beetle capacity is full.

When population density is low, beetles preferentially attack weakened or diseased trees (Gara et al. 1984; Powell et al. 1996). In the absence of other nesting beetles, we assume flying beetles prefer to land in areas with low resistance to attack, so base landing rate is:

$$r_{base} = r_b (1 - R)^{r_2} \tag{4}$$

R is a value between 0 and 1 that determines the relative resistance of trees to attack, r_b is the maximum possible landing rate of pioneer beetles, and r_2 controls the selectivity or preference for low resistance over high resistance areas. Landing rate increases as the number of nesting beetles (N)

increases, peaks at some intermediate number of beetles, and declines to zero as the number of nesting beetles reaches capacity (K) (Figures A.4 and A.5):

$$landing\ rate_{i,j,t} = [1 - (\frac{N}{K})^{r5}][r_{base} + (r_m - r_{base})(1 - e^{-r_1 \frac{N}{K}(1-R)^{r3}})] \quad (5)$$

r_m is the maximum possible landing rate, r_1 determines how fast landing rate increases with the number of nesting beetles, r_3 determines how the relative preference of flying beetles for low resistance areas persists as the number of nesting beetles increases, and r_5 determines the sensitivity of flying beetles to crowding.

The long-range attractive effects of trans-verbenol and the two multi-functional pheromones are modeled with a single attractive pheromone, A. Production rate (per beetle) is maximum (a_m) when nesting beetles are sparse, and decreases to zero as host capacity is reached. Total pheromone production rate (per time) at location *i,j* is (Figures A.6 and A.7):

$$pheromone\ production\ rate_{i,j} = Na_m(1 - \frac{1 + e^{a_1 R^{a6}(R^{a3}-1)}}{1 + e^{a_1 R^{a6}(R^{a3}-N/K)}}) \quad (6)$$

The beetle density at which pheromone production reaches one half of maximum increases with resistance, R, and the rate of increase is determined by a_3. The parameter a_1 determines the steepness of production decline, and a_6 ensures that initial per beetle pheromone production is the maximum unless host resistance is very nearly zero.

We have assumed that flying beetles keep aggregating and landing until areas are full, while nesting beetles stop actively producing aggregating pheromones as soon as host resistance is overcome. While these suppositions remain speculative, it is interesting to note that a conflict between the interests of flying and nesting beetles could account for the multi-functionality of frontalin and exo-brevicomin. In the interest of reducing competition, it makes sense that nesting beetles should put some resources toward producing an "antiaggregation" signal, rather than simply falling silent. However, flying beetles should interpret this signal as an indicator of a secure resource, and aggregate towards it until some threshold concentration is reached. If beetle behaviour is optimal, the concentration at which attractive pheromones become unattractive should correspond to the point at which the cost of competition equals the advantage of security. Finally, the rapid decay rate of verbenone (Kostyk et al. 1994) could explain why this pheromone functions only as an antiaggregant.

3.1.6. Pheromone diffusion and decay

Following Powell et al. (1996) we represent pheromone dynamics using a simple linear diffusion model with a constant decay rate, δ_a:

$$\frac{\partial A}{\partial t} = b_a \nabla^2 A + pheromone\ production\ rate_{i,j} - \delta_a A \quad (7)$$

The first term ($b_a \nabla^2 A$), known as the heat equation, is a standard model for approximating the aggregate behaviour of many particles that each move stochastically. The equation is used to describe the spread of heat or the diffusion of dissolved substances through a homogeneous medium. It is also used to model the stochastic (random walk) component of organism movement (Okubo 1980; Okubo and Levin 2001; Turchin 1998), and is the basis for the continuous approach to beetle dispersal modeling taken by Powell et al. in the MPBpde. b_a is known as the diffusion coefficient, and determines the rate of spread. In a random walk, $b_a = \lambda 2/2T$, where λ is step length and T is the period of time between two consecutive

moves. ∇^2 is the Laplacian operator. In discrete two-dimensional space, $\nabla^2 A$ (at grid cell x,y) is equal to the sum of differences in pheromone concentration between adjacent locations:

$$\nabla^2 A_{x,y} = (A_{x-1,y} - A_{x,y}) + (A_{x+1,y} - A_{x,y}) + (A_{x,y-1} - A_{x,y}) + (A_{x,y+1} - A_{x,y})$$

3.1.7. Complete model of dispersal, aggregation and attack

In sum, at any point in time, t, throughout the flight period, a mountain pine beetle k may be in one of five modes. Waiting beetles can emerge, flying beetles can become receptive to pheromones, receptive flying beetles can land (Equations 4 and 5), and all flying beetles can die (Table 2). The population of flying and nesting beetles at each location are F and N, respectively.

$$F_{i,j,t} = \sum_{k=1}^{\text{num beetles at i,j}} (\Omega_{k,t} = uflying) + \sum_{k=1}^{\text{num beetles at i,j}} (\Omega_{k,t} = rflying) \tag{8}$$

$$N_{i,j,t} = \sum_{k=1}^{\text{num beetles at i,j}} (\Omega_{k,t} = nesting) \tag{9}$$

At each time-step flying beetles can also change locations. The probability of an unreceptive beetle (*uflying*) moving to any adjacent location depends on the direction of that beetle's flight in the previous time-step (Equation 1). A receptive beetle (*rflying*) will follow a pheromone gradient (∇A) where such a gradient is present (Equations 2 and 3). Otherwise, it follows the same correlated random walk as unreceptive beetles (Equation 1). Finally, pheromones arise, spread, and decay according to Equations 6 and 7.

The model follows the MPBpde (Powell et al.) in overall structure; nesting beetles produce pheromones to which flying beetles respond, and landing rate, nesting success, and pheromone production depend on forest attributes. We also follow on a number of particulars, including: uniform emergence of beetles over the flight period; constant death rate of flying beetles; and pheromone dynamics modeled by simple diffusion with a constant decay rate.

This model differs from Powell et al. in several ways. First, flying beetles are modeled individually. The correlated random walk followed by unreceptive beetles or receptive beetles in the absence of pheromones (Equation 1) differs somewhat from the simple diffusion of flying beetles in the absence of pheromones in the MPBpde, but that difference is not particularly important. More crucial differences are in how forest is represented (R is static and K is new), how landing rate and pheromone production vary with forest attributes and crowding (Equations 4, 5 and 6), and how flying beetles interpret pheromones (Equations 2 and 3). See the preceding sections for reasoning behind the differences.

3.1.8 Extending the model over multiple years

To extend the model, we consider the attack efficiency of beetles. Provided trees are at least somewhat resistant, beetle success, measured as per capita reproductive rate, should be low when the density of nesting beetles is low, and increase as the number of nesting beetles increases enough to overcome host defenses. As the number of nesting beetles increases even further towards carrying capacity, per capita reproductive rate will decrease due to increasing competition (Safranyik 1999). Furthermore, the point at which host defenses are overcome and survival reaches the maximum should be the point at which pheromone production by nesting beetles declines (Figures A.8 to A.10):

$$reproduction\ rate_{i,j} = r_w\left(1 - \frac{(N/K)^{s_5}}{s_4}\right)\left(\frac{1 + e^{s_1 R^{s_6}(R^{s_3} - 1)}}{1 + e^{s_1 R^{s_6}(R^{s_3} - N/K)}}\right) \tag{10}$$

The parameters s_1, s_3, and s_6, control the relationship between reproductive rate and resistance the same way that a_1, a_3, and a_6 control the relationship between pheromone production and resistance. r_w determines the maximum per capita reproductive rate in the absence of resistance or competition, which we refer to as the winter production rate. s_4 determines the minimum reproductive rate that flying beetles will tolerate (or the reproductive rate at carrying capacity); once an area has reached carrying capacity, flying beetles will always choose to keep searching for less crowded habitat (landing rate goes to zero). s_5 determines the rate at which reproductive success decreases due to crowding.

The number of emerging beetles year n+1 is then (Figures A.8 to A.10):

$$\gamma_{i,j,n+1} = N_n(reproduction\ rate_{i,j,n}) \tag{11}$$

If trees have no resistance, the proportion of trees killed at a location is equal to the proportion of trees attacked. Given the simplifying assumption that beetles fill trees to capacity before moving on, the kill rate is given by N/K. If trees have resistance, then the kill rate will be less than N/K. We assume the decrease is equal to the ratio of realized reproduction rate to maximum reproduction rate. Realized reproduction rate is given by Equation 10, and maximum reproduction rate is the realized rate when R = 0. Dividing through, we get (Figures A.8):

$$kill\ rate_{i,j} = \frac{N}{K}\frac{(1+e^{s_1 R^{s6}(R^{s3}-1)})}{(1+e^{s_1 R^{s6}(R^{s3}-N/K)})} \tag{12}$$

As trees are killed, capacity declines by the kill rate:

$$K_{n+1} = K_n(1 - kill\ rate_n) \tag{13}$$

However, assuming that surviving trees fully recover before the next flight period, and all trees within a stand have the same relative resistance, resistance within the stand R remains constant over the course of the outbreak. In truth, trees within a stand may vary widely in their resistance to mountain pine beetles, and resistance also varies over time as trees age (Shrimpton and Thompson 1983; Thomson 1987), weather conditions change (Thomson and Shrimpton 1984; Thomson et al. 1984), or mortality changes stand density (Amman et al. 1988; Amman and Logan 1998).

3.1.9. Base model parameterization

In a field study designed to parameterize the MPBpde, Biesinger et al. (2000) found that the average number of nesting beetles in colonized trees ranged from 567 to 1496 MPB tree^{-1}. Stands susceptible to mountain pine beetle attack typically range from between 750 to 1500 stems ha^{-1} (Shore and Safranyik 1992; Whitehead et al. 2001). An average stand density of 1000 susceptible stems ha^{-1} suggests an average beetle capacity on the order of 1,000,000 MPB ha^{-1}. For computational efficiency, we model "individual" groups of 1000 beetles that emerge and move together. This may increase the efficiency of spread at the margins of the infestation, but as long as aggregation of several groups of beetles is required for success the error should be acceptable. To avoid confusion we present all results and parameter values in thousands of MPB, or kMPB. Thus, the average carrying capacity, K_0, is 1000 kMPB ha^{-1}.

Following Powell et al., we assume some variability in forest composition over space so that weak, low capacity areas can provide foci for attack. Beetle capacity is uniformly distributed with a mean of 1000 kMPB ha^{-1}, a minimum of 500 kMPB ha^{-1}, and a maximum of 1500 kMPB ha^{-1}. We also assume that resistance varies normally across the landscape, with a mean of 0.5, and a standard deviation of 0.3. Again, actual resistance among stands is a complex phenomenon dependent on age and composition

of stands, and weather (Amman et al. 1988; Amman and Logan 1998; Shrimpton and Thompson 1983; Thomson 1987; Thomson and Shrimpton 1984; Thomson et al. 1984).

Before adding the complications of chemotaxis, it is worthwhile to consider how beetles move in the absence of guidance. Together, the parameters K_o, R_o, ω_1, r_f, α_m, r_b, r_2, and the beetle step rate Δt determine the distance traveled by beetles across a contiguously forested landscape in the absence of pheromones. Following Biesinger et al. (2000), we use a constant death rate (ω_1) of 0.01 fh^{-1}. (The base unit of time in this analysis is the flight-hour, fh.) There are approximately 5 fh per day, because beetles only fly during the heat of the day. We do not model the resting period between each flight day; in this model beetles fly continuously through the flight period. The free flight duration of mountain pine beetles is not known, but related bark beetle species require an average of between 30 and 90 minutes flight exercise before becoming receptive to olfactory stimuli (Borden et al. 1986). Lacking better estimates, we assume that beetles become receptive to pheromones at a rate (rf) of 0.65 fh^{-1}. Finally, beetles turn an average of angle, α_m, of 35° at each step. See Figure A.1 for the effect of α_m on the distribution of turning angles.

In the study from which Biesinger et al. (2000) derived the MPBpde movement parameter estimates, Turchin and Thoeny (1993) found that 50 % of southern pine beetles disperse less than 0.69 km, and 99% disperse less than 3.29 km. A step rate (Δt) of 0.25 fh $cell^{-1}$ (where each raster cell is 50 × 50 m or 0.25 ha) and a maximum base landing rate (r_b) of 0.2 fh^{-1} gives an average travel distance of 0.64 km on contiguous habitat, and 1.3 km on a landscape without habitat (but note that the latter may be an underestimate due to edge effects – see Figure 5 for details). 90% of beetles travel less than 1.5 km on contiguous habitat (Figure 5).

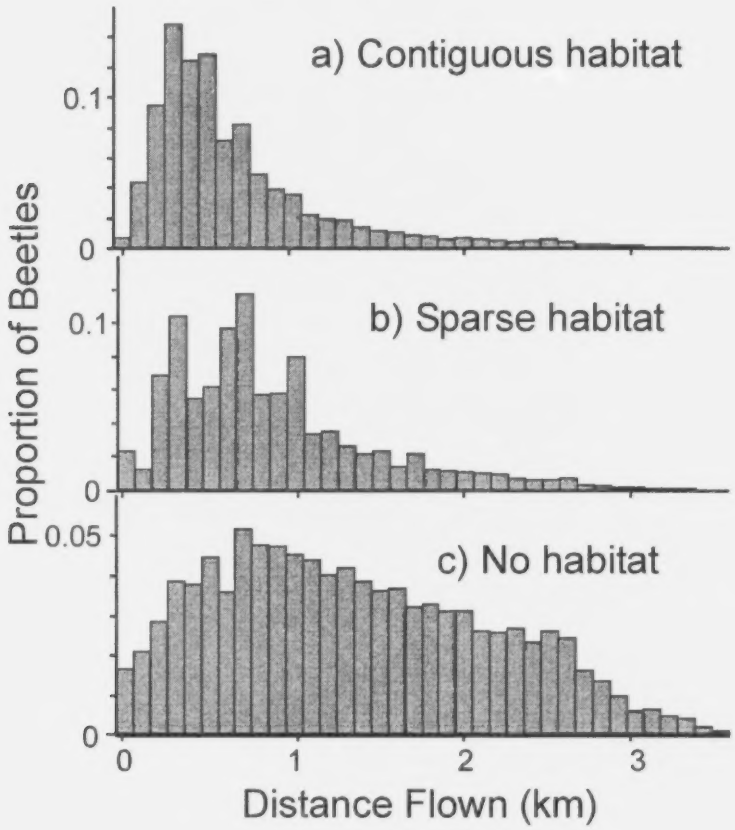

Figure 5: Distances flown by modeled mountain pine beetles in the absence of pheromones on a) contiguous habitat (100% of the landscape suitable for landing) b) sparse habitat (10% of the landscape suitable) and c) no habitat (0% of the landscape suitable). In the first two cases beetles can either die or land, but in the absence of habitat flight distance is limited by death alone. The average flight distance on contiguous habitat is 0.64 km, and the median is 0.48 km. With no habitat the average flight distance is 1.3 km, and the median is 1.2 km. Note that beetles cannot fly more than 3.5 km from their source at the centre pixel because the square landscapes are only 5 km across. The flight distance distributions suggest that when habitat is available edge effects are not severe, but in the absence of habitat they are more so.

Biesinger et al. (2000) estimate that pheromones are produced at a rate of 20 μg fh^{-1} $kMPB^{-1}$, diffuse at an average of $b_a = 0.648$ ha fh^{-1}, and decay at an average rate of $\delta_a = 180$ fh^{-1} in a stand of average openness with a wind speed of 0.6 m s^{-1}. We accept these base diffusivity and decay rate estimates, and assume a maximum pheromone production rate, a_m, of 20 μg fh^{-1} $kMPB^{-1}$. Following Geiszler et al. (1980), we assume that beetles are sensitive to concentration of pheromone greater than 3×10^{-3} ng m^{-3}. We further assume chemicals more than 3 m from the ground are lost to the system, so the minimum detectable pheromone concentration is $a_r = 0.1$ μg ha^{-1}. On a grid cell resolution of 0.25 ha, these spread parameters give a radially symmetric pheromone plume shown in Figure 6. The prediction that beetles can only communicate effectively over distances less than 50-100 m is supported by experience with pheromone baited trapping, where baits should be set no more than ~75 m apart to be most effective (Borden, J. personal communication).

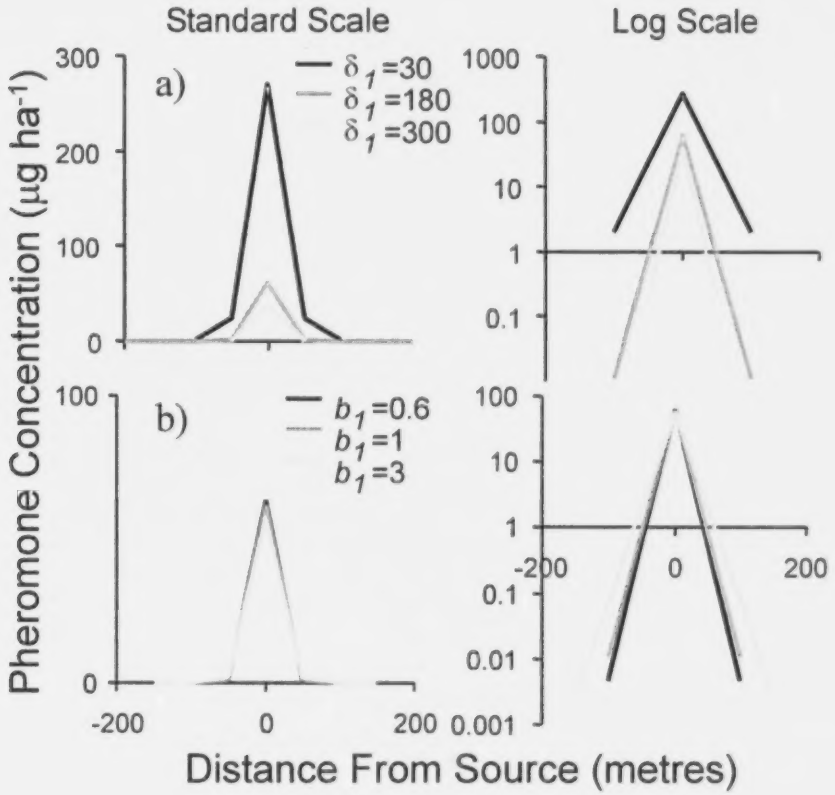

Figure 6: Sensitivity of pheromone plume size and shape to a) pheromone decay rate (δ_1) and b) pheromone diffusivity (b_1). The number of nesting beetles, N, is 3/5 of carrying capacity (K).

Reproduction, pheromone production, and landing parameters remain to be specified. We first assume that pheromone production declines to zero as reproductive rate increases to maximum (see Figures A.4-A.7 for landing and pheromone production curves). Thus, the parameters that control the reproduction and pheromone production curves are equal ($a_1 = s_1$, $a_3 = s_3$, and $a_6 = s_6$). Similarly, landing rate declines with reproduction rate, so $r_5 = s_5$ and per area beetle production rate is maximum when beetles are at capacity (N = K), implying that $s_4 = s_5+1$. The ratio of emerging to attacking beetles must be at least greater than 1 for the population to increase. We select $r_w = 3.5$ for the base case.

We chose the pheromone sensitivity parameters a_1 and a_2, the production parameters s_1, s_3, s_5, and s_6, and the landing parameters r_1 and r_3 so that beetles effectively aggregate, aggregation is important for success, and the beetle success and landing curves look reasonable (Figures A.4-A.10). For a complete description of all parameters and their associated baseline values, see Table 3.

3.1.10 Numerical methods and model implementation

The mixed reaction-diffusion and individual-based modeling approach limits implementation options. Software well equipped to solve partial differential equations is not well designed to represent individuals, and tools helpful for individual-based modeling do not include more advanced mathematical capacities. To resolve this dilemma without excessive programming difficulty, we used an explicit first order forward-Euler method to solve the diffusion equations. This method is less accurate and has more restrictive stability conditions than other methods, but can be implemented without the use of sparse-matrix solvers

or other mathematical tools. As long as the following criterion is met, the method is stable (Sewell 1988):

$$\Delta t_a \leq \frac{1/4H}{b_a}$$

Δt_a is the pheromone time-step, H is the grid cell resolution, and b_a is the diffusion coefficient for pheromones. Accuracy of the solution is not a primary concern because neither our model nor our questions are precise; we care about whether beetles can communicate over 50 or 200 m, not the precise shape of the diffusion curve.

We implemented the model using SELES, a declarative modeling language for spatio-temporal modeling (Fall and Fall 1999; Fall and Fall 2001 — note that the language has been expanded to allow individuals since the original release). Reflective boundary conditions are assumed throughout.

3.1.11 Temporal extent and resolution

Pheromones decay at a rate of 180 fh^{-1} and spread at a rate of 0.648 ha fh^{-1} (Biesinger et al. 2000), suggesting that pheromone dynamics must be resolved at time step of less than 1/180 fh. In contrast, beetles move at a rate of 1 ha fh^{-1}, and land or die at a rate of less than 1 fh^{-1}, suggesting that a time-step of 1/4 fh is adequate to resolve beetle dynamics. To speed computation, White and Powell (1998) solve the pheromone equations analytically over the beetle time step. We follow the spirit of this approach, but, lacking the tools required for transformation to Fourier space, we solve the pheromone equation numerically. After each beetle time-step we simulate pheromone dynamics until the chemical landscape is near enough to equilibrium that further simulation causes changes of less than 10-3 μg ha^{-1} in chemical concentration, and then proceed to the next beetle time step.

Following Logan et al. (1998) we assume a baseline flight period of 8 days with 5 fh per day, giving a total annual flight period, p_f, of 40 fh in which all beetles disperse. Note that the duration of flight period in any year depends on weather and local conditions, and can vary from 3 days to 3 weeks (Safranyik et al. 1978). We ran each simulation for 25 years, which was long enough for beetles on contiguous habitat to successfully kill all susceptible trees. Beetle dynamics are resolved with a time-step of $\Delta t = 0.25$ fh. Pheromones dynamics run on a time-step of $\Delta t_a = 1/500$ fh.

3.1.12 Initial conditions

We begin each run with 1,250,000 successful beetles in the center of each landscape, giving an initial emergence rate of $1250 r_w / p_f = 109.375$ kMPB fh^{-1} from the center pixel.

3.2 Clarifying hypotheses

The underlying hypothesis is that beetles are constrained by pheromone connectivity, which is in turn influenced by the pattern of the forest mosaic. That is, infestations should spread efficiently between patches near enough to one another that pheromones can travel from one to the other, and slowly or not at all across larger gaps.

To measure how landscapes are connected by pheromones, we join patches less than communication distance from one another into connected clusters (Keitt et al. 1997). Since beetles spread from the center in all landscapes, we measure only the center cluster (Figure 7). If beetle spread is strictly limited by whether or not beetles can communicate across gaps then the final extent of the infestation should be equal to the center cluster size in each landscape. We analyzed the effect of experimental factors on center cluster size using mixed models (see the method for analyzing g_w and d_w).

In general, the effect of increasing any of habitat compaction (p), patch size (w), and communication distance (or buffer width, d) while holding the others constant is to either increase center cluster size (ccs) or leave it unchanged. Interactions between variables are significant ($ccs \sim d*w*p$, n=320, $p<0.0001$ – Note: throughout the remainder of this document, the notation "response ~ factor1*factor2" followed by a sample size (n) and a p-value indicates that these two factors significantly interact in their effect on the response variable. Sample sizes are for both within and between-subject factors, but all factors except p and w are within-subject so the number of independent samples is less than n. The three possible response variables are abbreviated as: ccs = centre cluster size, kr = kill rate, and op = outbreak probability. The two kill rate parameters (g_w and d_w) are treated as repeated measures of the same response (kill rate - kr). rpt is the factor name associated with the two dependent variables (g_w and d_w). A significant effect of rpt indicates that the two kill rate parameters (g_w and d_w) differ in their response to the experimental factors).

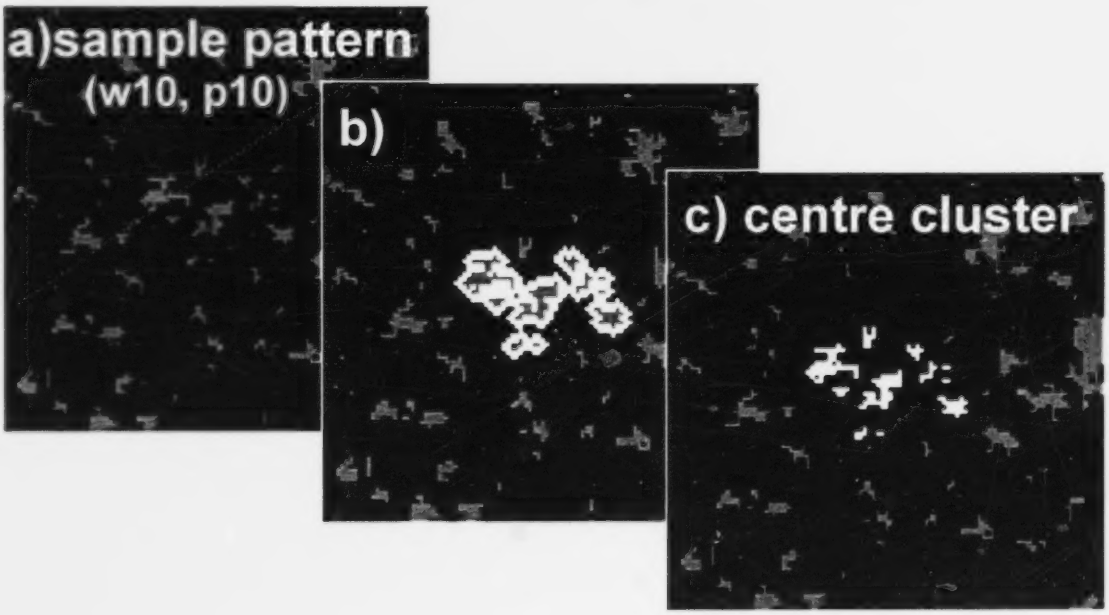

Figure 7: Definition and calculation of center cluster size. Patches nearer together than communication distance (200 m, in this case) are joined to delineate connected "clusters" of habitat (b). The centre cluster consists of the habitat patch at the centre of the landscape, and all habitat patches to which it is connected (c). Center cluster size is the sum of habitat area within this cluster.

When patch size is small (w0) and communication distance is large (d = 200 m), the distance between patches is less than 200 m, so the landscape is connected (center cluster size ~100%) regardless of habitat compaction level (Figure 8). Increasing habitat compaction decreases the distance between patches enough to move the landscape from almost completely unconnected to completely connected when communication distance is intermediate (Figure 8, w0, d = 50 m/100 m). When communication distance is zero, the effect of habitat compaction is insufficient to connect the landscape (Figure 8, w0, d = 0 m).

When patch size is small, the transition from connected to unconnected occurs over a relatively small range of habitat compaction (10-20%), demonstrating the threshold-type behaviour characteristic of percolation networks (Figure 8, w0). As patch size becomes larger (w10 - w50), the distance between patches becomes both larger and more variable. As this happens, differences between communication distance levels tend to diminish (Figure 8). The effect of habitat compaction also becomes more continuous, and the threshold effect disappears.

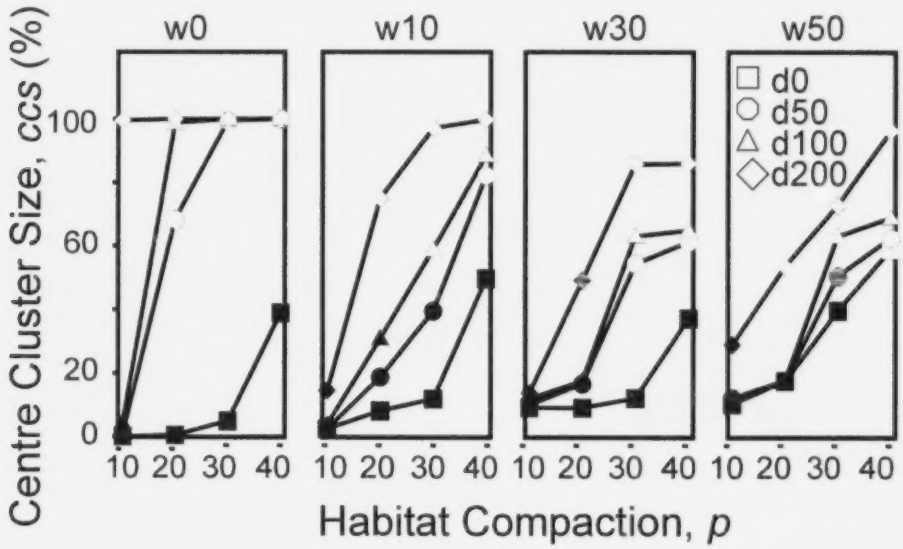

Figure 8: The effect of habitat compaction (area over which habitat is dispersed, p), patch size (w), and communication distance (buffer width, d) on centre cluster size (ccs). If infestations can only spread efficiently over habitat gaps across which beetles can communicate, then centre cluster size should predict final infestation extent. These show the experimental effects expected if this hypothesis is correct. Overall, the interaction between all three variables is significant (p=0.0001). Open symbols show group means that are not significantly different from the maximum (250 ha), while closed symbols indicate no significant difference from the minimum. Group means marked with stripes are significantly different from both the maximum and the minimum. Each point marks the mean value for five replicate patterns.

3.3 Experiment I – base case

The questions are: What is the effect of patch size and patch compaction on infestation spread rate and extent, and how does pheromone communication distance alter these effects? Is beetle success directly constrained by pheromone connectivity, and can beetles aggregate efficiently only over gaps across which they can communicate?

Pheromone communication distance can be altered by adjusting one of two parameters in the model. All else being equal, decreasing pheromone diffusivity (b_a) and increasing decay rate (δ_a) both decrease the extent of a pheromone plume. Diffusivity has a relatively small effect on plume extent (Figure 9), so we only changed decay rate. To see how the effect of pattern varies with communication distance we vary pheromone decay rate across three levels. d50 is 0-50 m, d100 is 50-100 m, and d200 is 100-200 m (Figure 9). We expect that both outbreak frequency and kill rate (g_w, d_w) should increase with increasing habitat compaction, communication distance, or patch size. Interactions between variables should be like those in Figure 8.

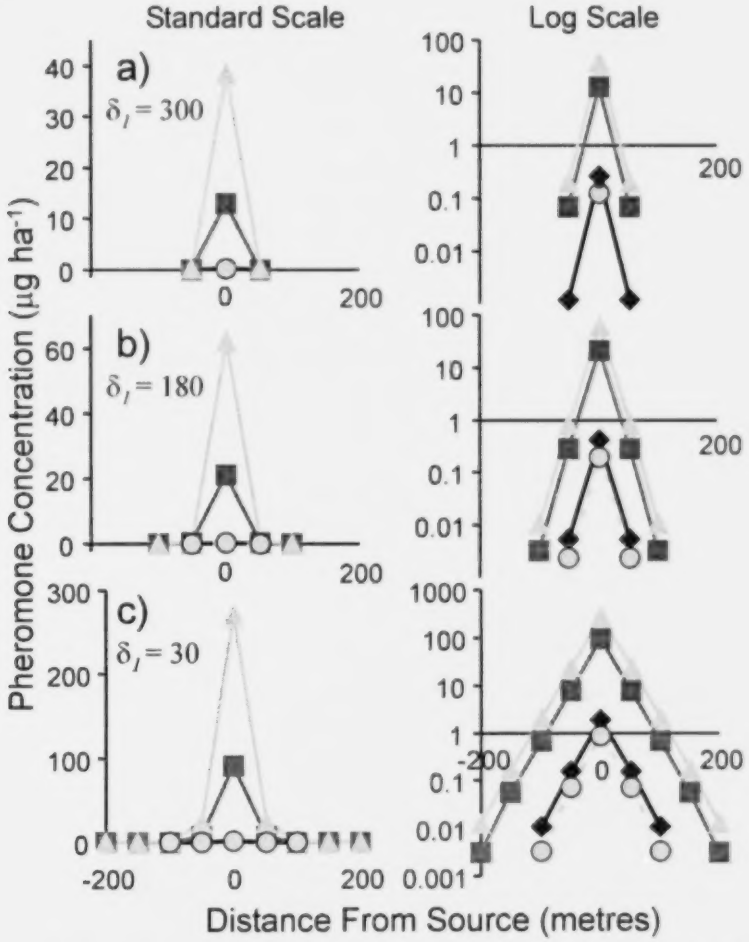

Figure 9: Pheromone plumes used in base experiment. Graphs a) through c) show how changing pheromone decay rate (δ_1) alters the relationship between pheromone plume size and shape and the number of nesting beetles, N. △: N = 0.001*K, ■: N = 0.2*K, ◆: N = 0.6*K, ○: N = 0.996*K. A decay rate of $\delta_1 = 300$ (a), given a communication distance of 0-50 m (d50), $\delta_1 = 180$ (b) gives a distance if 50-100 m (d100), and $\delta_1 = 30$ (c) gives a distance of 100-200 m (d200).

The effect of habitat compaction on kill rate is significant ($kr \sim p$, n = 240, p=0.003), and kill rate generally increases with habitat compaction as expected (Figure 10). The interaction between communication distance and the two response variables (g_w, d_w) is also significant ($kr \sim d^*rpt$, n = 240, p<0.0001). Increasing communication distance from 50 to 100 m consistently increases kill rate as expected. However, increasing communication distance from 100 to 200 m only appears to increase kill rate when habitat compaction is low (Figure 10). When habitat compaction is high, kill rate tends to decrease as communication distance increases from 100 to 200 m. This apparent interaction between habitat compaction and communication distance is not significant ($kr \sim d^*p^*rpt$, n = 240, p=0.0701), but the trend is consistent over all patch sizes. Kill rate appears to increase slightly with patch size, especially when communication distance is small (d50), but this effect is also not significant ($kr \sim w$, n = 240, p=0.077).

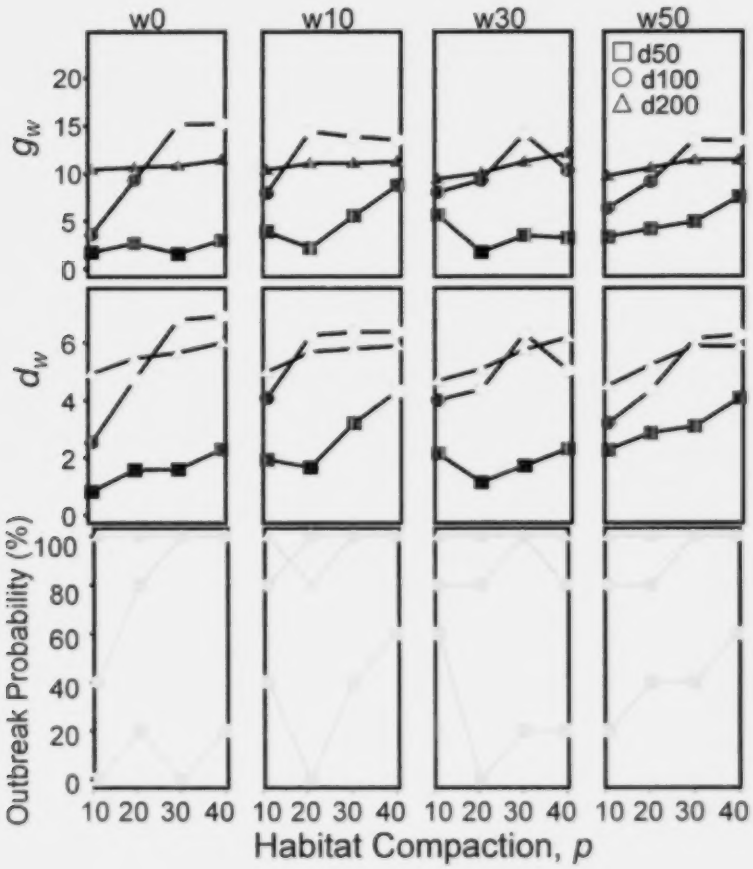

Figure 10: The effect of habitat compaction (p), patch size (w) and communication distance (d) on kill rate (g_w, d_w) in the base case. Note that the interaction between communication distance and response variable is significant (p<0.0001), as is the effect of habitat compaction (p=0.0003), but the effect of patch size is not. Open symbols show group means that are not significantly different from the maximum, while closed symbols indicate no significant difference from the minimum. Groups marked with stripes are not significantly different from either the maximum or the minimum. Outbreak probabilities are shown for interest, but the data could not be analyzed in this form due to lack of variation when communication is maximum (d200).

In general, trends in outbreak probability mirror trends in kill rate, except that kill rate may vary between cases where outbreak probability is consistently 100% (Figure 10). However, relationships between outbreak frequency and the experimental factors are not significant (Figure 11). Experimental results are summarized in Table 4.

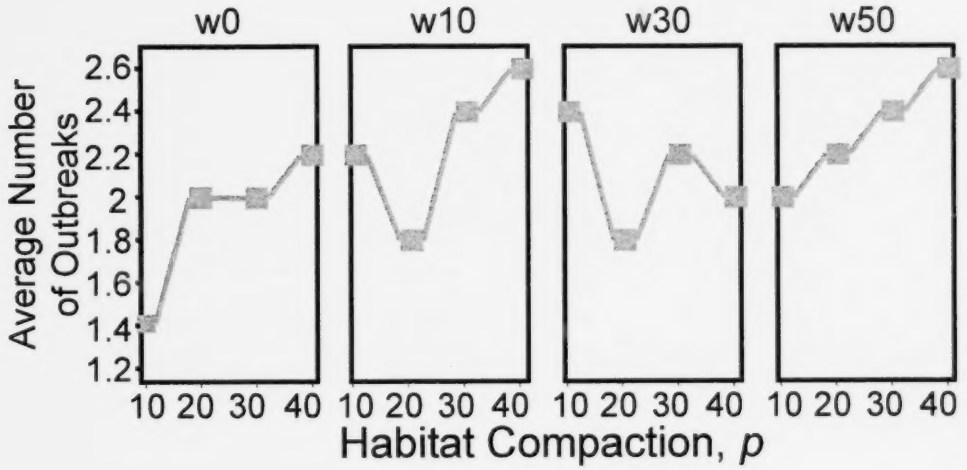

Figure 11: The effect of habitat compaction (p) and patch size (w) on the average number of outbreaks (op) in the base case. Outbreaks are tallied across three levels of communication distance for each pattern, so the maximum number of outbreaks possible is 3, and the minimum is 0. However, no landscape had less than 1 outbreak in this case because outbreaks always occurred when communication distance was large. Patch size (w) and habitat compaction (p) do not have a significant effect on the average number of outbreaks.

3.4 Experiment II – the effect of free flight

The question is: How does the tendency of beetles to fly for some time before becoming responsive to pheromones alter the results from Experiment I? To answer this question, we repeat the Experiment I with no free flight period (r_f=4) and a reduced pattern set (w0 and w50 only).

We expect that without free flight, center cluster size might be more likely to constrain infestation size because beetles are less likely to fly towards areas without attractants as they do in free flight. Overall, we expect that free flight should be advantageous to beetles.

The effect of free flight on kill rate varies with response variable (g_w or d_w) and communication distance ($kr \sim r_f^* d^* rpt$, n=240, p<0.0001), with response variable (g_w or d_w) and habitat compaction ($kr \sim r_f^* p^* rpt$, n=240, p=0.0486), and with communication distance and patch size ($kr \sim r_f^* d^* w$, n=240, p=0.0053) (Figure 12). Removing free flight also increases the frequency of outbreaks overall ($op \sim r_f^* rpt$, n=20, p<0.0001) (Figure 13). Essentially, removing free flight eliminates all experimental effects by increasing spread rate and outbreak frequency when communication distance is small, and decreasing spread when communication distance is intermediate and habitat compaction is high (Figure 12).

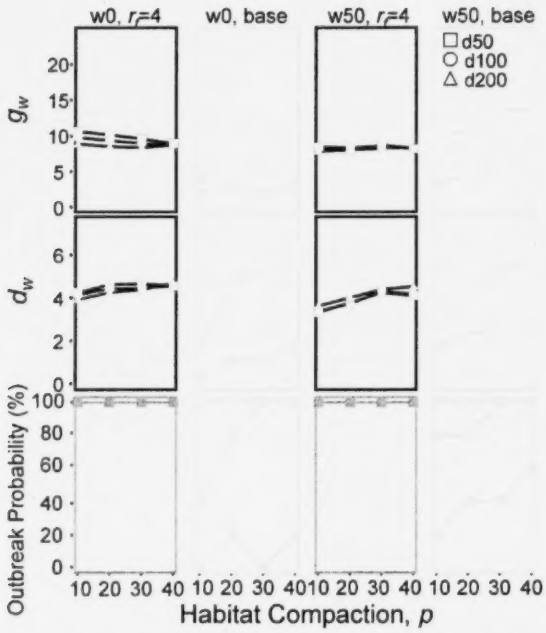

Figure 12: The effect of habitat compaction (p), patch size (w), communication distance (d) and free flight (r_f) on kill rate (g_w, d_w) in Experiment II. Note that the interaction between patch size, communication distance, and free flight is significant ($p = 0.0053$), as is the interaction between free flight, response variable and habitat compaction ($p = 0.0486$) and the interaction between free flight, response variable and communication distance ($p < 0.0001$). Grey panels are repeated from Figure 10, shown here for comparison. See Figure 10 for more explanation.

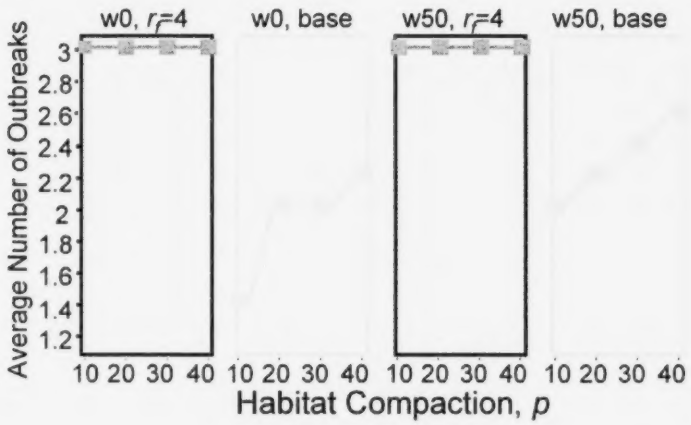

Figure 13: The effect of habitat compaction (p), patch size (w) and free flight (r_f) on the average number of outbreaks (op) in Experiment II. Note that outbreak frequency increases significantly with free flight (r_f) status ($p<0.0001$), but no other experimental effects are significant.

3.5 Experiment II extension – sensitivity without free flight

Overall, kill rate in the absence of free flight is very high (Experiment II). Does habitat compaction, communication distance or patch size have an effect if overall reproductive rate is not so high? To test the effect of decreased overall success on the relationship between success and habitat compaction in the case with no free flight we repeated Experiment II with a lower reproductive rate (r_w=3). We expect that when kill rate is not uniformly high, kill rate and outbreak frequency should depend on habitat compaction, communication distance, and patch size.

Decreasing winter reproductive rate (r_w) significantly alters the relationship between kill rate and habitat compaction, and this effect varies significantly with patch size ($kr \sim r_w * w * p$, n=240, p<0.0124) (Figure 14). Decreasing r_w also alters the relationship between kill rate, communication distance, patch size and response variable (g_w and d_w) ($kr \sim r_w * d * w * rpt$, n=240, p<0.0002) (Figure 14). Decreasing reproductive rate also decreased the frequency of outbreaks overall ($op \sim r_w * rpt$, n=20, p<0.0001) (Figure 15). Essentially, when both reproductive rate and patch size are small, kill rate and outbreak probability increase with both patch size and habitat compaction as expected (Figure 14 and 15). Increasing patch size largely eliminates these effects.

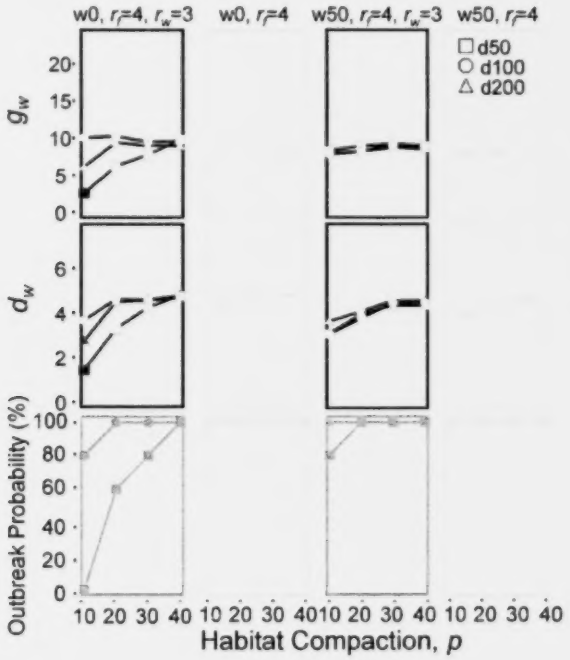

Figure 14: The effect of winter reproductive rate (r_w) on the results from Experiment II. The interaction between reproductive rate (r_w), communication distance (d), patch size (w), and response variable (d_w, g_w) is significant (p=0.0002), as is the interaction between habitat compaction (p) and response variable (d_w, g_w) (p<0.0001) and the interaction between reproductive rate (r_w), patch size (w) and habitat compaction (p) (p=0.0124). Symbols are filled as in Figure 10.

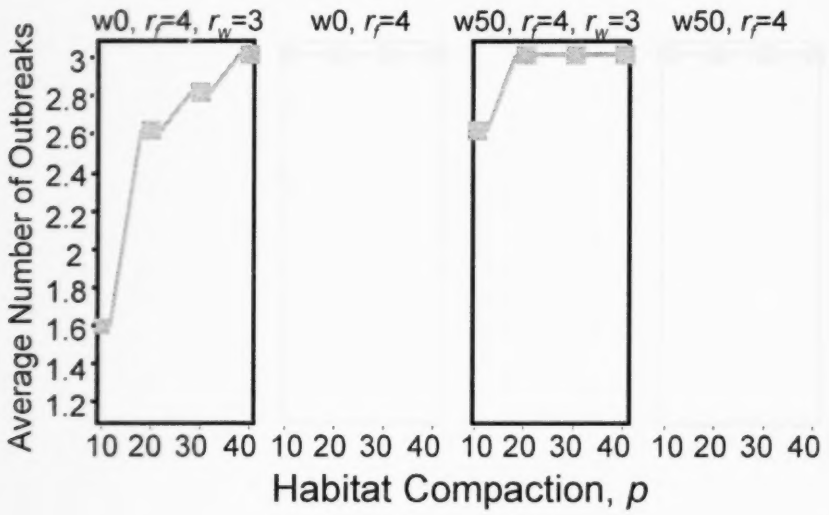

Figure 15: The effect of winter reproductive rate (r_w) on the results from Experiment II. Outbreak frequency increases significantly with free flight (r_f) status ($p<0.0001$), and no other experimental effects are significant.

4.0 Discussion

4.1. Beetle ecology

Before considering what the results of this study say about mountain pine beetles, it is worth asking whether model behaviour is reasonable. First, the striking result from Experiment II is that beetles with a free flight period outbreak less often and less quickly. In general, biologists are well advised to be wary of claims that behaviour should be advantageous just because it is done (Gould and Lewontin 1979). However, since the trait is common but not ubiquitous among beetle taxa, and variable within beetle populations (Borden et al 1986), it seems most prudent to assume free flight is advantageous under at least some circumstances, and to be wary of a model that predicts otherwise. One problem might be that we allow unreceptive beetles to die, but not land. Our free flight period is perhaps too long in some circumstances, and dispersal during the free flight period might not be random. In general, we presume that real free flight behaviour is more subtly formulated to help beetles avoid overcrowding while not making them lost. Free flight may also have other functions not addressed by the model.

Model behaviour is unrealistic in several other ways: real beetles can easily spread over 250 ha in 4 or 5 years, rather than 9 or 10; and real beetles often do not kill 100% of susceptible trees. Given the simplicity of the model, the number of uncertain parameters and relationships, and the limited amount of sensitivity analysis and calibration, we expect a model such as this to be more useful as a tool to explore our state of knowledge and assumptions, and to make general rather than precise predictions.

At face value, the prediction is that beetles are relatively insensitive to small-scale landscape heterogeneity because they have a free flight period. A more cautious conclusion is that the spatial dynamics of infestation spread at small scales can depend strongly on relatively minor details of dispersal behaviour, such as free flight. All beetle dispersal models omit a great deal of detail, and most have omitted free flight. Readers and modelers should be aware of this omission.

We began with a model developed by others, then considered the assumptions underlying that model, and the consequences for our particular question. Working from another model made us more acutely aware of our own assumptions, and the challenges to be overcome. We differ from the MPBpde on two main points other than the inclusion of a free flight period. First, we assume that beetles continue to attack trees in an area until all susceptible hosts are killed. In the MPBpde, there is no explicit link between the pheromone concentration at which an area becomes unattractive and the point at which landing rate declines to zero, so areas with very low resistance (and therefore low beetle capacity) might never become unattractive, while areas with high resistance might become unattractive before host resistance is overcome.

Our second concern was that a flying beetle in an area with no trees, ringed on all sides by areas full of nesting beetles will tend to remain in place, even though there is nowhere for it to land. In contrast, we assume the antiaggregants discourage beetles from landing, but not from dispersing through an area. Beetles also may fly above the canopy to avoid overcrowding (Safranyik 1978; Safranyik et al. 1989; Safranyik et al. 1992).

This work required that we clarify expectations about what scale of landscape heterogeneity might affect beetles. Since pheromones are only effective over 50 or 100 m, the possibility is that patchiness at quite small scales may be important. Although we have used the term "landscape", in forestry management the question is about patchiness within, rather than between, forest stands.

Ultimately, questions about the effect of pattern on beetles can only be answered by experimentation. Experimentally manipulating forest "landscapes" tens or hundreds of kilometers across is difficult. Forest stands, on the other hand, are quite manageable experimental units. Indeed, there have been a number of harvesting experiments that indicate thinned stands are less susceptible to mountain pine beetles (Cahill 1978; Cole et al. 1983; Mitchell et al. 1983; Waring and Pitman 1985; McGregor et al. 1987; Amman et al. 1988; Mitchell 1994). Thinning is one extreme in a range of forest harvest options. Exploring the

effects of a wider range of cutting patterns is both feasible and potentially interesting. Finally, note that the nature of the non-susceptible area probably makes a difference: pheromone plumes are more likely to be disrupted by turbulent air in open areas than under a forest canopy.

It would be theoretically interesting to see how the susceptibility of patchy stands differs from both thinned and unharvested stands. It might also be operationally useful. Even though thinning is known to reduce stand susceptibility, it is difficult and expensive, and thus not extensively done. Cutting larger patches may be more operationally feasible.

4.2. Movement modeling

Others have recognized that organisms often deviate from random walk or correlated random walk movement patterns (Okubo 1980; Levin 1992; Turchin 1998; Okubo and Levin 2001), but the consequences of deviation have not been systematically studied. Real-world successes with correlated random walks and related diffusion approximations indicate that these models are robust to some behavioural complexity, and more general than their simplicity suggests (Levin 1992; Turchin 1998). However, the strong effect of free flight here indicates that not all behavioural complexity is without consequence. It would be interesting to better understand the limits of diffusion and correlated random walk models, and the types of behaviour that render these models inadequate.

Rather than testing arbitrary possibilities, it is probably more productive to focus on understanding the behaviour of particular organisms in particular situations. However, studies of the dispersal of particular organisms do not automatically contribute to more general understanding. Thus far, general insight from individual-based models has been hampered by lack of systematic reference to theory and lack of a common framework that would make it possible to meaningfully compare models (Turchin 1998; Grimm 1999; Grimm et al. 1999). In response, some authors have advocated a hierarchical approach, where understanding is sought by comparing the behaviour of simple models to those incrementally more complex (Turchin 1998; Grimm et al. 1999). We have attempted this approach, and agree that it is a fine ideal. We note, however, that many of the criticisms of individual-based modeling (and spatio-temporal simulation in general), while valid, are not easily addressed. Although many simulation efforts would benefit from more comprehensive experimentation and more systematic reference to the framework of classical theoretical ecology (Grimm 1999), such attempts should proceed with a realistic view of the technical and computational challenges. Spatial simulation is computationally demanding.

Apart from theoretical concerns and concerns over inadequate data, complex individual-based models have been criticized because they are hard to develop, hard to communicate, and hard to understand (Grimm et al. 1999). Individual-based models implemented with general purpose programming languages have been plagued by software bugs, awkward software design, and general incomprehensibility (Grimm et al. 1999). In response to these challenges, a number of software tools have been developed to help separate the details of model form from model implementation, and thus make implementation, verification and communication easier (Lorek and Sonnenschein 1998, 1999; Fall and Fall 2001). We did not try alternative methods for implementing this model, so cannot compare their relative merits. Anecdotally, the process of incremental component testing and experimentation was greatly aided by the SELES modeling tool (Fall and Fall 1999; Fall and Fall 2001). We draw particular attention to the possibility for discrete entities (individual beetles) and continuous quantities (pheromones) to spread and change at different time-scales in the same model, as this is the first such "mixed" model implemented in SELES to be published.

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Tables

Table 1a: Definitions of terms from landscape ecology.

Landscape ecology terms	
landscape	Area that is spatially heterogeneous in at least one factor of interest (Turner et al. 2001).
cell	In this study, land is represented as matrix (raster) of square cells. Each cell characterized by a spatial location (row and column) and the spatial resolution (50 by 50 m). Landscape attributes (e.g. suitability of habitat for beetles or the number of beetles at a given time) are spatially homogeneous within cells.
scale	The spatial or temporal dimension of an object or process, characterized by both grain (or resolution) and extent (Turner et al. 2001). For example, the (spatial) extent of our landscapes is 5 km by 5 km, and the resolution is 50 m by 50 m. The (temporal) extent of our simulations is 20 years, and the temporal resolution of the mountain pine beetle dynamics differs from the temporal resolution of the pheromone dynamics.
habitat	Cells that contain at least some pine that is susceptible to beetles are classified as habitat.
patch	In general, surface area that differs from its surroundings in nature or appearance, or, on a gridded landscape, a contiguous group of cells of the same mapped category (Turner et al. 2001). In this paper, the mapped category of interest is suitability for beetles (habitat or non-habitat). We use an 8-neighbour rule, so diagonally adjacent cells are considered to be touching one another.
spatial heterogeneity/ patchiness	In general, complexity and variability of a system property in space (Li and Reynolds 1994). System properties that may vary on our binary (habitat/non-habitat), gridded landscapes include the size and shape of patches. The most homogenous possible landscape is one where habitat cells are distributed uniformly across the landscape, and a landscape where cells are distributed randomly also has low heterogeneity. Heterogeneity increases as cells are grouped together into patches of varying size and complexity. We also informally refer to spatial heterogeneity in this context as patchiness.
spatial autocorrelation	If a variable is spatially autocorrelated then the relationship among the values of a given variable is a function of the spatial distances between them or their locations in space. Hence, the notion of spatial dependence implies that there is a lack of independence among data from nearby locations. Spatial autocorrelation is estimated by comparing the value of a variable at one location with those at given distances apart (termed spatial lag or distance interval) (Fortin and Dale 2005). Positive spatial autocorrelation at short lag distances indicates that similar values are grouped together in space.
fragmentation	The breaking apart of habitat into smaller patches, or patches separated by greater distance.
cluster	A cluster consists of one or more patches that are less than some threshold distance apart from one another (Keitt et al. 1997). In this case, the threshold distance of interest is the distance across which beetles can effectively communicate (communication distance).

Table 1b: Definitions of terms from population ecology and terms specific to this paper.

Population ecology terms	
infestation/ outbreak	Mountain pine beetle population dynamics are characterized by endemic periods, when beetles persist in low numbers and kill few trees, interspersed with periods of rapid population increase, when beetles kill many trees. Loosely, we refer to a rapid rise in beetle population and damage in one area as an ***infestation***. If local infestations arise in many areas independently or spread affect larger areas, this landscape-level phenomenon is an ***outbreak***.
aggregation/ congregation	Turchin (1998) defines aggregation as population redistribution that leads to an uneven spatial distribution of organisms so that some spatial localities are characterized by elevated population densities (aggregations) and others by decreased density. In contrast, congregation is aggregation as a result of behavioural responses of organisms to conspecifics. Thus, to ***congregate*** means to gather ***together***; as opposed to ***aggregate***, which is to gather ***at*** some locality. Congregating organisms may respond to neighbours using visual, acoustic, or chemical (pheromones) stimuli, or indirectly to population density cues, such as feeding damage on a host plant. According to this definition, mountain pine beetles congregate. However, aggregation is the term commonly used in mountain pine beetle literature, so we use the term aggregative to describe beetle dispersal.
Terms specific to this paper	
communication distance	Communication distance is the distance across which pheromones effectively spread and beetles effectively communicate (Section 1.4).
habitat compaction	Habitat compaction increases as the area across which (a fixed amount of) habitat is dispersed decreases (Section 2.2.1). As habitat compaction increases the distance between patches decreases, given constant patch size and shape.
centre cluster size	Centre cluster size is the area of habitat within the cluster at the centre of each landscape (Section 3.2). In simulation runs, infestations originate in the centre of the landscape. If beetle spread is strictly limited by whether or not beetles can communicate across gaps then the final infestation extent should be equal to the centre cluster size in each landscape.
free flight	Free flight is a period of flight before beetles become receptive to pheromones (Section 1.3.3).
nesting beetle	Nesting beetles are beetles that have committed to staying at a location. In reality, once beetles have landed, they may decide to resume flying if a tree seems unsuitable. For simplicity, we only consider a beetle to be nesting once it has both landed and decided to remain at a location (Section 3.1.2, 3.1.5).

Table 2: Probabilities for transitions between five beetle modes. Each beetle can be either waiting to emerge, flying and unreceptive to pheromones or kairomones (uflying), flying and receptive to pheromones and kairomones (rflying), nesting once they have landed, or dead, and each beetle may undergo one mode transition per beetle time-step Δt. pf is the length of the annual flight period (in hours), ω_f is the death rate of flying beetles (per hour) and r_f is the rate at which unreceptive free flying beetles become receptive to pheromones (per hour). The landing rate of flying beetles at each location (landing rate$_{i,j}$) depends on the number of nesting beetles (N), host capacity (K) and host resistance (R) at that location. See text for more detailed explanation.

Beetle Mode at Time t-Δt \ Beetle Mode at Time t	waiting	uflying	rflying	nesting	dead
waiting	$1-\Delta t/p_t$	$\Delta t/p_t$	0	0	0
uflying	0	$1-\Delta t\ \omega_1 - (1-\Delta t\ \omega_1)\Delta t\ r_f$	$(1-\Delta t\ \omega_1)\ \Delta t\ r_f$	0	$\Delta t\ \omega_1$
rflying	0	0	$1-\Delta t\ \omega_1 - (1-\Delta t\ \omega_1)\Delta t$ (landing rate$_{i,j}$)	$(1-\Delta t\ \omega_1)\Delta t$ (landing rate$_{i,j}$)	$\Delta t\ \omega_1$
nesting	0	0	0	1	0
dead	0	0	0	0	1

Table 3: Model parameters and their associated base values. Units are: µg = 10-6 grams; ha = hectare; fh = flight-hour; kMPB = thousands of mountain pine beetles.

Parameters	Description	Base Value	Units	Source
Landscape				
P_1	initial beetle population	1250	kMPB	arbitrary
R_0	average initial resistance	0.5	..	arbitrary
R_{dev}	standard deviation of initial resistance	0.3	..	arbitrary
K_0	average initial carrying capacity	1000	kMPB	Biesinger et al. 2000
K_{dev}	maximum deviation of initial carrying capacity from average initial carrying capacity	500	kMPB	arbitrary
M	spatial extent	100	cells	reasoning
H	spatial resolution	0.25	ha cell^{-1}	reasoning
Time				
p_f	length of annual flight period	40	fh year^{-1}	Logan et al. 1998
Δt	beetle time step	0.25	fh	reasoning
Δt_a	pheromone time step	1/500	fh	reasoning
Flight				
α_m	approximately average turning angle in the absence of pheromones	35°	degrees	arbitrary
a_1	pheromone sensitivity parameter	1.3	..	arbitrary
a_r	minimum detectable pheromone concentration	0.1	µg ha^{-1}	Geiszler et al. 1980
a_s	pheromone sensitivity parameter	4	..	arbitrary
r_f	free flight parameter	0.65	fh^{-1}	Borden et al. 1986
Landing				
r_m	maximum possible landing rate	0.8	fh^{-1}	arbitrary
r_b	maximum pioneer landing rate (landing = r_b when R = 0 and N = 0)	0.2	fh^{-1}	arbitrary
r_1	controls the rate at which landing increases with N	20	..	arbitrary

Table 3 continued on the following page.

Table 3 continued:

Landing continued...				
r_2	controls the effect of R on pioneer landing rate	2	..	arbitrary
r_3	determines the persistence of preference for low R areas as N increases	0.3	..	arbitrary
r_5	controls the rate at which landing decrease with crowding	4	..	arbitrary
Pheromone				
a_m	maximum possible pheromone production rate	20	µg ha^{-1}	Biesinger et al. 2000
a_1	controls the rate at which pheromone production declines with N	20	..	arbitrary
a_3	determines the effect of R on the N value at which pheromone production reaches half of maximum	0.3	..	arbitrary
a_6	ensures that beetles that land in areas with no resistance (R = 0) do not produce pheromones, but beetles that land anywhere else produce pheromones at maximum rate until resistance is overcome.	0.001 (very small)	..	reasoning
b_a	pheromone diffusivity	0.685	ha fh^{-1}	Biesinger et al. 2000
δ_a	pheromone decay rate	180	µg ha^{-1}	Biesinger et al. 2000
Survival				
ω_1	flying beetle death rate	0.01	fh^{-1}	Biesinger et al. 2000
r_w	maximum per capita beetle reproduction rate, referred to as winter reproductive rate ($F_{waiting,n}/N_{n-1}$)	3.5	$year^{-1}$	arbitrary
s_1	controls the rate at which beetle success increases with N	a_1	..	reasoning
s_3	determines the effect of R on the N value at which beetle success reaches half of maximum	a_3	..	reasoning
s_4	determines the average reproductive rate at carrying capacity (N = K)	$r_5 + 1$	..	reasoning
s_5	determines the rate at which reproductive success decreases to minimum as N approaches K.	r_5	..	reasoning
s_6	ensures beetles landing in areas with no resistance reproduce at maximum, but beetles landing elsewhere are not successful unless resistance is overcome.	a_6	..	reasoning

Table 4. Summary of experimental results. Abbreviations: Experimental factors are denoted by *w* (patch size), *p* (habitat compaction), and *d* (communication distance). *kr* indicates overall kill rate response, *rpt* refers to response variable (*gw* or *dw* – if *rpt* is significant then *gw* and *dw* differ in their response to the experimental factors), and *op* is overall outbreak probability. Other parameters are as in Table 3. n: Two sample sizes given for each experiment are the number of model runs (between*within subject factors) and, in brackets, the number of landscape instances (between subject factors only). Design: All experiments are have fully crossed factorial designs. For example, "kr ~ d|w|p" indicates that all independent effects (*d*, *w*, *p*) and all possible interactions (d^*w, d^*p, w^*p, d^*w^*p) were tested for. Test Results: Only significant interactions are shown. Statistical p values are distinguished from habitat compaction references by italics, bolding, and context. Summary of Effects: Up (↑), down (↓) or sideways (↔)arrows indicate positive, negative or neutral relationships, respectively, between the response variable (right side) and the experimental factor (left side). Notably strong and consistent effects are shown in bold (⇑). Effects that are conditional upon the value of other factors are qualified with the key word given, followed by a list of conditions. For qualitative variables, the keyword when followed by one or more conditions indicates that response in these conditions is higher (↑) or lower (↓) than in other conditions.

Experiment	n	Design	Test Results	Summary of Effects	Notable Results
I base case Section 3.3, Figures 9 and 10	240 (80)	kr ~ d | w | p | rpt op ~ w | p	kr ~ d*rpt, $p < 0.0001$ kr~p, $p = 0.0003$ no op effects significant	kr ⇑ d kr ↑ p	• no effect of patch size (*w*) • effect of patch compaction (*p*) not as strong as expected.
II the effect of free flight Section 3.4, Figures 11 and 12	240 (40)	kr ~ r_f | d | w | p | rpt op ~ r_f | w | p	kr ~ r_f* d* rpt, $p < 0.0001$ kr ~ r_f * p* rpt, $p = 0.0486$ kr ~ r_f * d* w, $p = 0.0053$ op ~ r_f, $p < 0.0001$	when r_f = base, effects are as in Experiment I. kr ⇑ *when* $r_f = 4$ *given* d=0-50 kr ↑ *when* $r_f = 4$ *given* d=50-100 and p<30 kr ↓ *when* $r_f = 4$ *given* d=50-100 and p>20 kr ↓ *when* $r_f = 4$ *given* d=100-200 op ⇑ *when* $r_f = 4$	• free flight (r_f=base) disadvantageous to beetles unless communication distance (*d*) is high, or communication distance is low and patch compaction is also low. • effect of communication distance (*d*) and patch compaction (*p*) not robust to absence of free flight (r_f=4).
II extension sensitivity without free flight Section 3.5, Figures 13 and 14	240 (40)	kr ~ r_w | d | w | p | rpt op ~ r_w | w | p	kr ~ r_w* d* w* rpt, $p = 0.0002$ kr ~ p* rpt, $p < 0.0001$ kr ~ r_w* w* p, $p = 0.0124$ op ~ r_w, $p < 0.0001$	kr ⇑ p *given* r_w=3, w0, d=0-50 kr ↑ p *given* r_w=3, w0, d=50-100	• patch compaction (*p*), patch size (*w*) and communication distance (*d*) effects significant in the absence of free flight (r_f=4) when overall success rate is reduced.

Appendix

This appendix contains further information about the form of model equations.

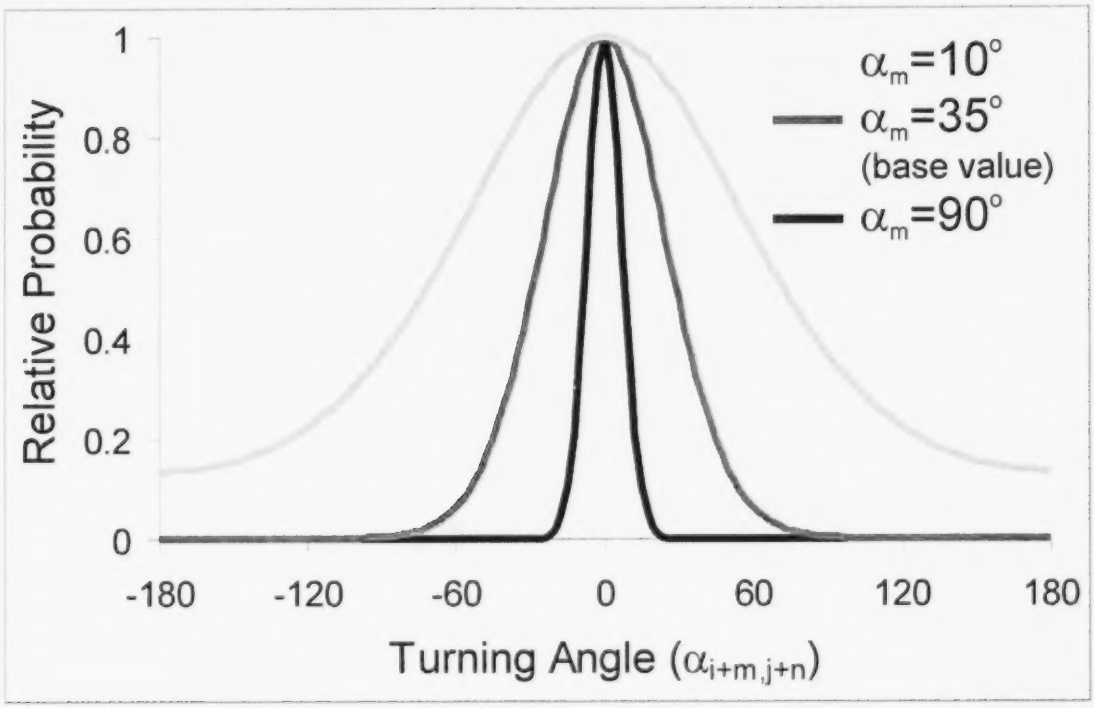

Figure A.1: Effect of α_m on the distribution of mountain pine beetle turning angles in free flight or the absence of chemical attractants (Equation 1). The quantity (1-cos($a_{i+m,j+n}$)) is exponentially distributed with parameter α_m, which is approximately equal to the average turning angle when α_m is small (~<60°). Average turning angle does not continue to increase indefinitely with α_m because the finite range of possible turning angles truncates the exponential distribution.

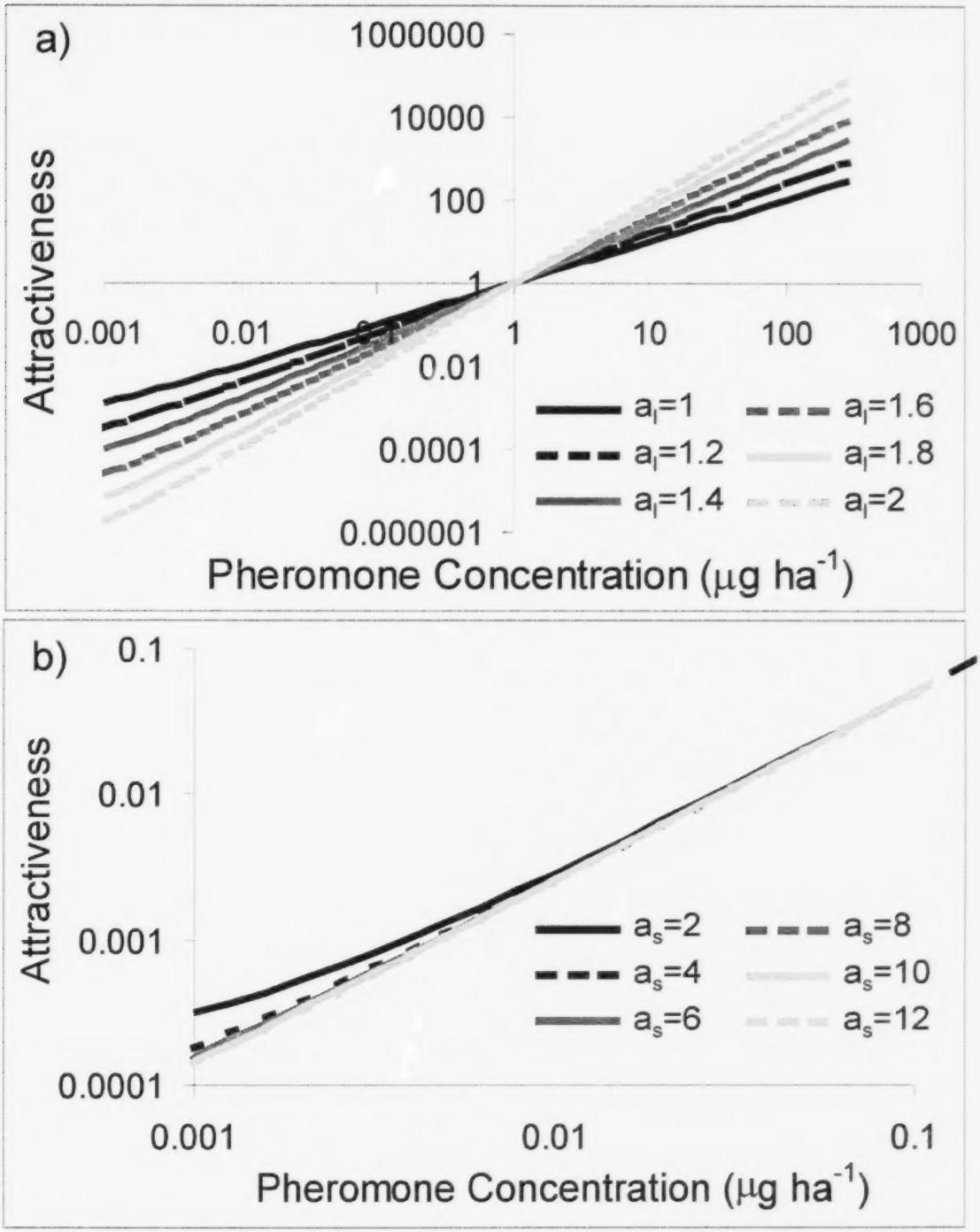

Figure A.2: The sensitivity of attractiveness to the gradient sensitivity parameters, a_l (a), and a_s (b) (Equation 3). The attractiveness parameter, a_p controls the sensitivity of mountain pine beetles to pheromone gradients, and a_s determines the relative preference of beetles for low pheromone over no pheromone areas.

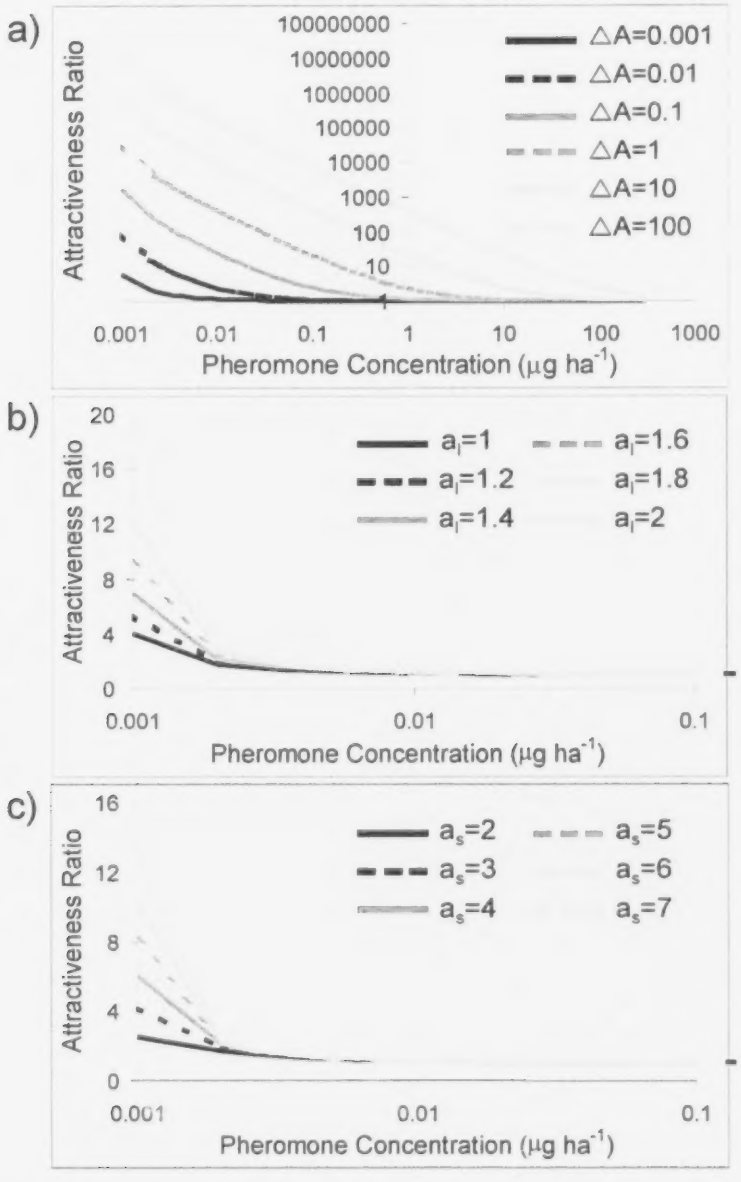

Figure A.3: Sensitivity of the relative attractiveness of pheromones to gradient size (ΔA) and gradient sensitivity parameters a_i and a_s (Equations 2 and 3). The probability a beetle will choose high pheromone location over a lower pheromone location is given by the attractiveness ratio, ($Attractiveness_{high}$/ $Attractiveness_{low}$). The attractiveness ratio depends on (a) the difference in pheromone concentration between the two locations (ΔA), (b,c) the attractiveness parameters a_i and a_s, and the base pheromone concentration (x-axis). The attractiveness function is designed so that beetles are more sensitive to differences in pheromone concentration when pheromone concentrations are low.

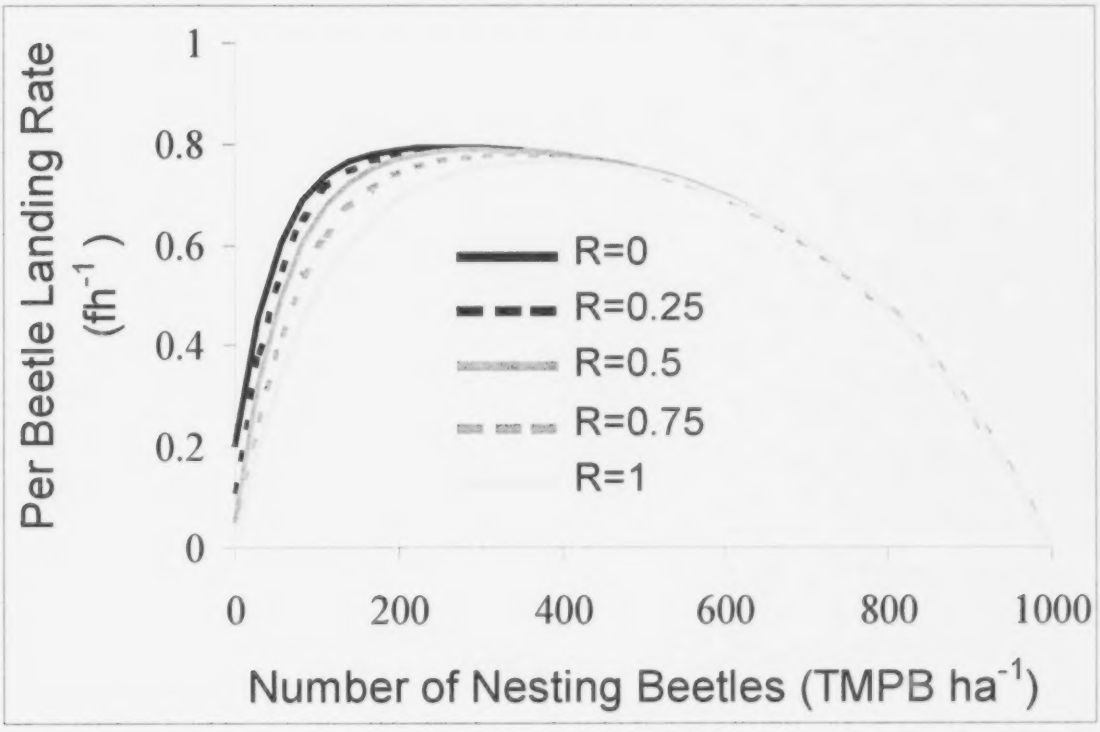

Figure A.4: Sensitivity of the relationship between per beetle landing rate and the number of nesting beetles (N) to host resistance (R) (Equations 4 and 5). Carrying capacity K is set to 1000 kMPB ha^{-1} in this example.

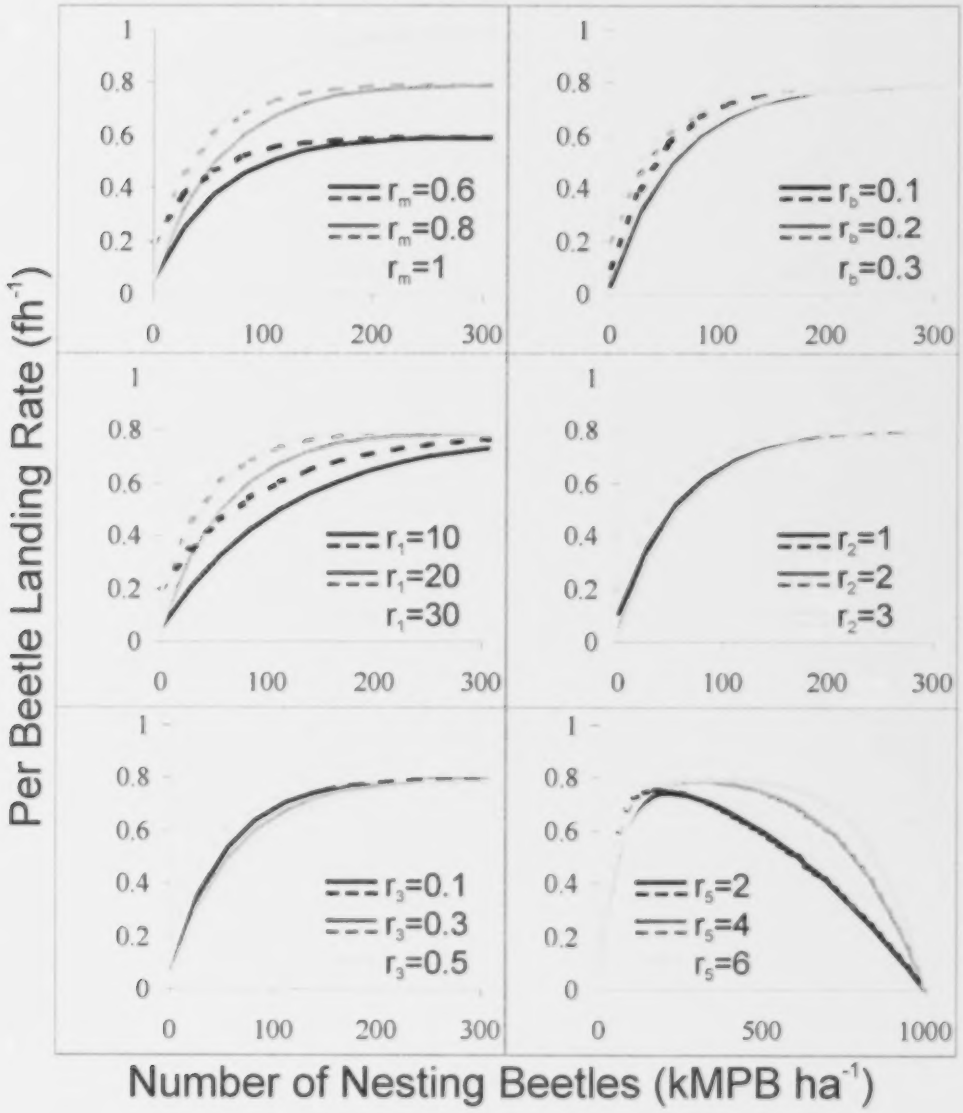

Figure A.5: Sensitivity of landing rate to six model parameters (Equations 4 and 5). Solid lines indicate the case where resistance (R) is 0.5. Dotted lines indicate R = 0. r_b is the maximum possible landing rate of pioneer beetles, r_m is the maximum possible landing rate, r_1 determines how fast landing rate increases with the number of nesting beetles, r_2 controls the preference of beetles for low resistance areas, r_3 determines how the relative preference of flying beetles from low resistance areas persists as the number of nesting beetles increases, and r_5 determines the sensitivity of flying beetles to crowding.

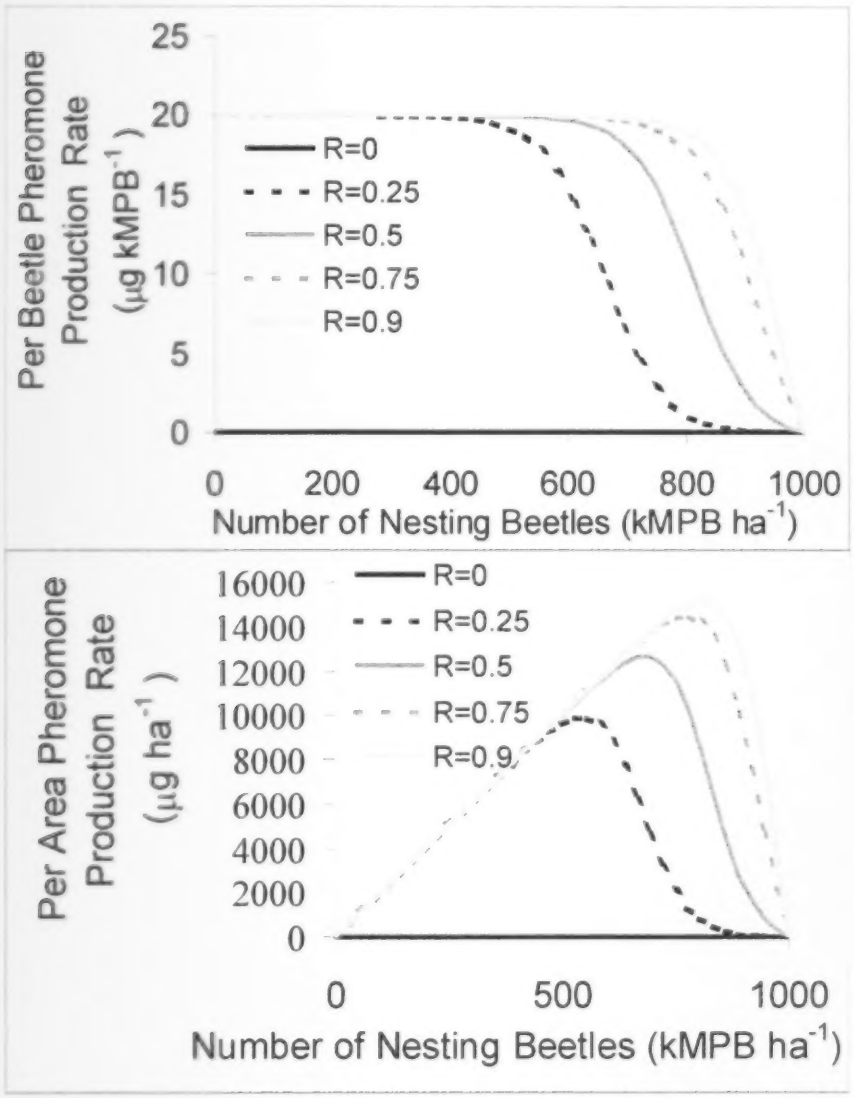

Figure A.6: Sensitivity of per beetle and per area pheromone production rates to host resistance (R) (Equation 6).

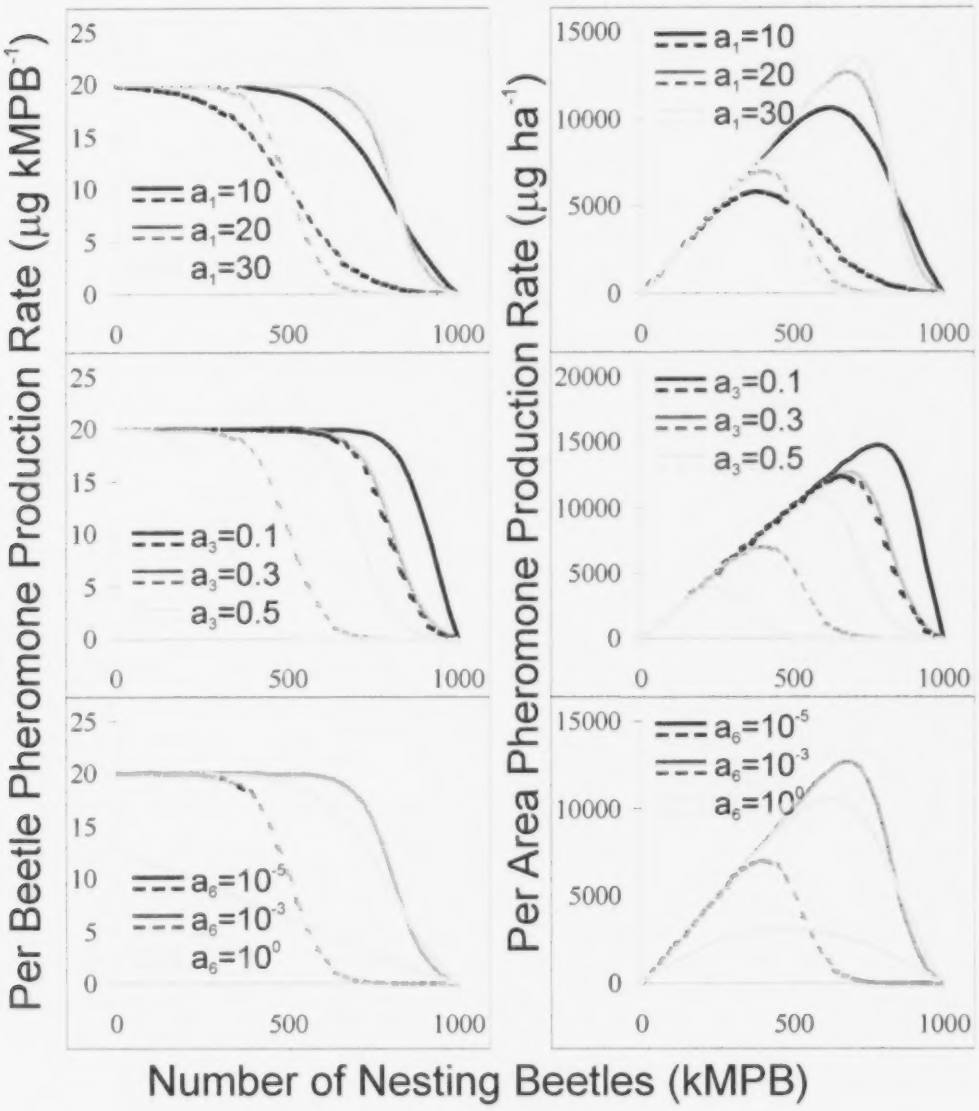

Figure A.7: Sensitivity of per capita and per area pheromone production to three model parameters (Equation 6). Solid lines indicate the case where resistance (R) is 0.5. Dotted lines indicate R = 0. a_1 determines the steepness of production decline, a_3 determines the rate of increase, and a_6 ensures that initial per beetle pheromone production is maximum unless host resistance is very near zero.

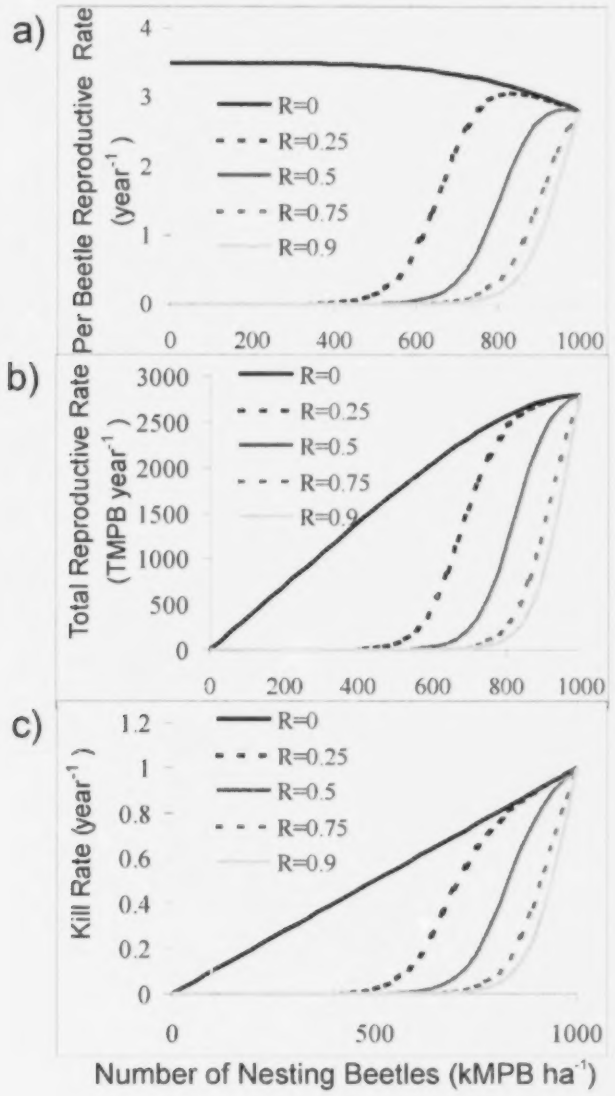

Figure A.8: Sensitivity of (a) per capita reproductive rate, (b) total reproductive rate, and (c) forest kill rate to host resistance (R) (Equations 10-12).

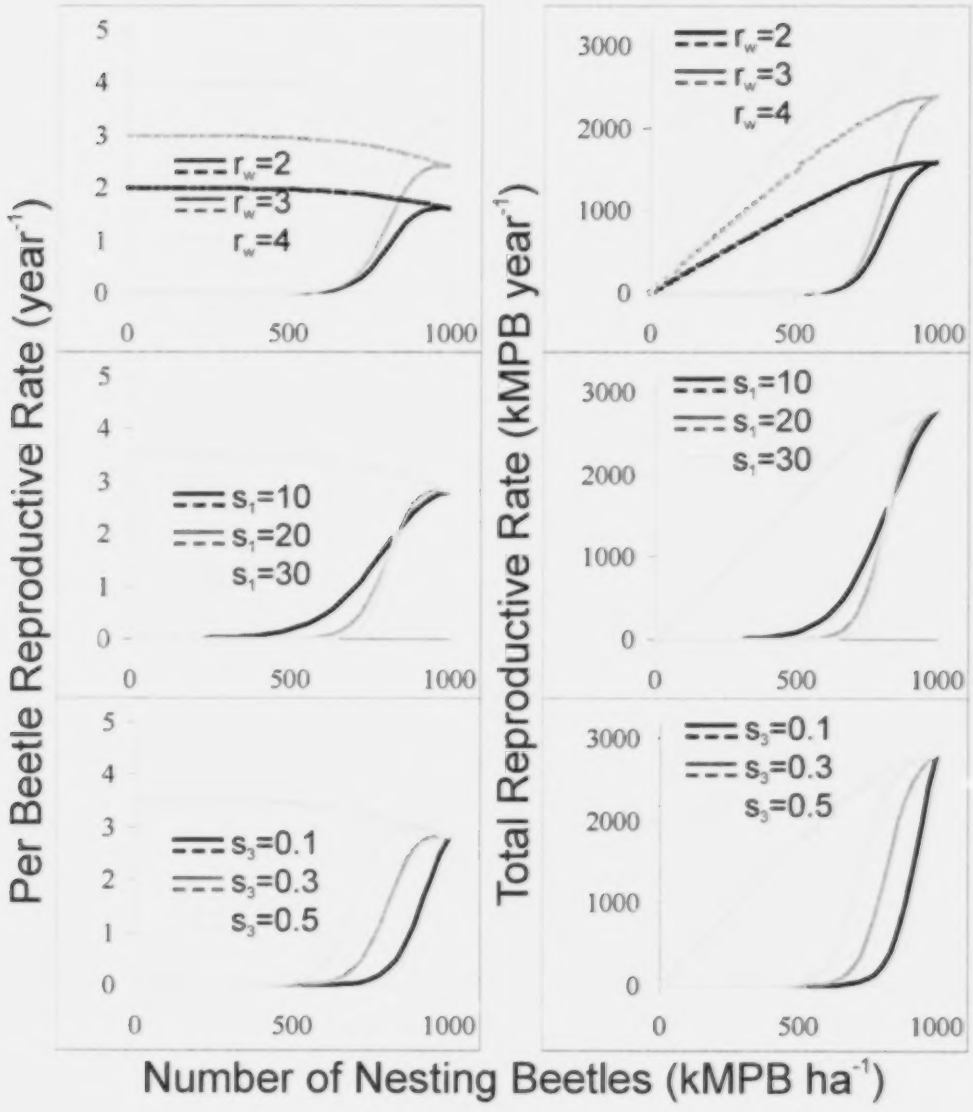

Figure A.9: Sensitivity of per capita and per area reproductive rate to three model parameters (Equations 10 and 11). r_w determines the maximum per capita reproductive rate in the absence of resistance or competition, and s_1 and s_3 together determine how strongly beetle success is impacted by host resistance. Solid lines indicate the case where resistance (R) is 0.5. Dotted lines indicate R = 0.

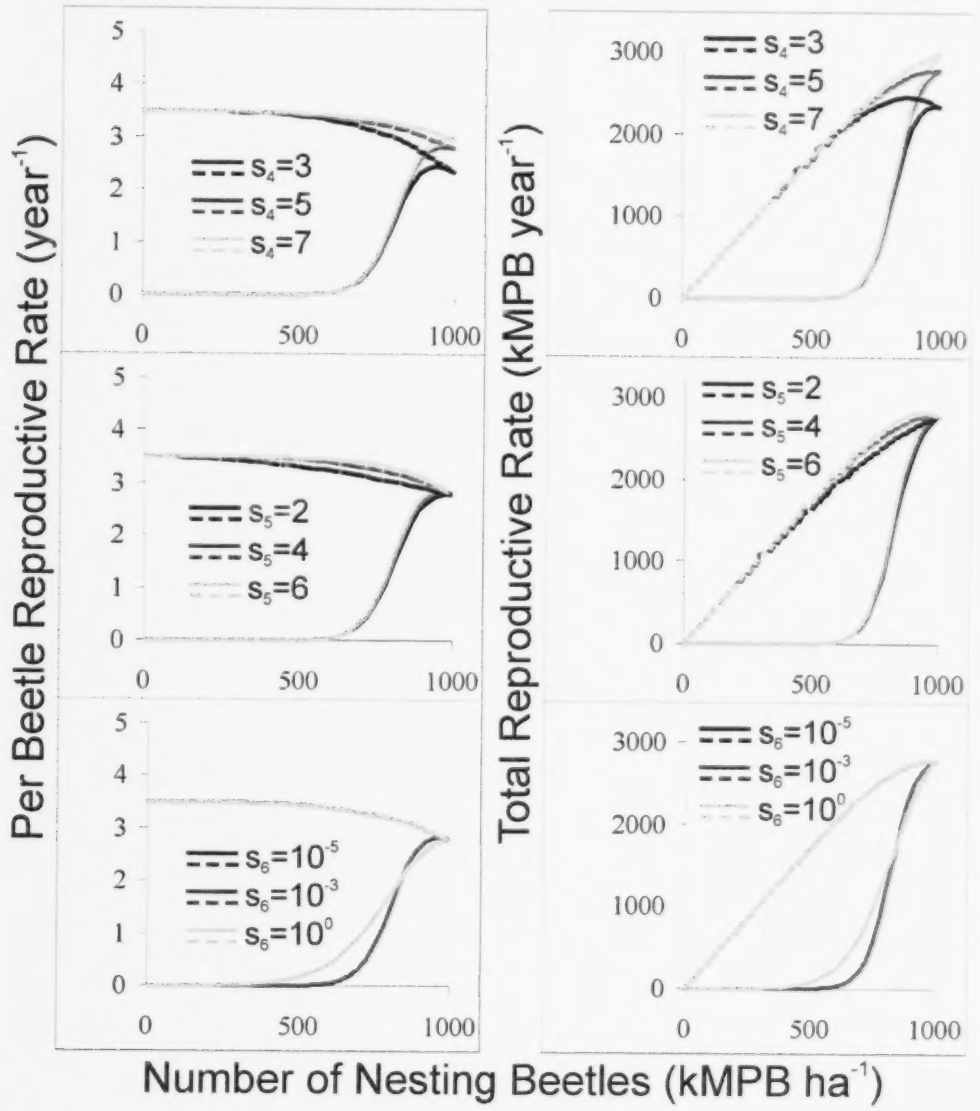

Figure A.10: Sensitivity of per capita and per area reproductive rate to 3 model parameters (Equations 10 and 11). s_4 determines the reproductive rate of beetles at carrying capacity, s_4 determines the rate at which reproductive success decreases due to crowding, and s_6 ensures that beetles are not successful unless there are enough beetles to overcome host resistance. Solid lines indicate the case where resistance (R) is 0.5. Dotted lines indicate R = 0.

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